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# The role of epibenthic predators in structuring marine soft-bottom communities along an estuarine gradient

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# THE ROLE OF EPIBENTHIC PREDATORS IN STRUCTURING MARINE SOFT-BOTTOM COMMUNITIES ALONG AN ESTUARINE GRADIENT

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by

Rochelle Diane Seitz

1996

**APPROVAL SHEET**

This dissertation is submitted in partial fulfillment of

the requirements for the degree of

Doctor of Philosophy

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Dedicated in loving memory of my dad, Roger Michael Seitz, who inspired me through example to achieve all of my dreams

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## PREFACE

Benthic community structure in marine hard-bottom habitats can be regulated by recruitment processes, interspecific competition, predation, and physical disturbance which vary along gradients of environmental stress. In contrast, the regulation of community structure in soft-bottom systems has been extensively studied, but a unifying theory of regulating forces remains elusive. In this dissertation, I (1) reviewed models of benthic community regulation, (2) examined the role of predation in structuring marine benthic communities in two zones along a salinity gradient, (3) examined effects of predation on a common and abundant bivalve, and (4) determined an appropriate community regulation model for this soft-bottom community. Specifically, predation intensity was manipulated experimentally in the field along a salinity gradient to quantify its impact upon benthic diversity as well as survival of a dominant infaunal prey species, *Macoma balthica*.

In the introductory chapter I reviewed the theoretical literature, which emphasizes studies in the rocky intertidal zone, on community regulation in marine benthic systems, and I modified the Menge and Sutherland (MS) model to incorporate soft-bottom communities (Chapter 1). Next, I presented results from manipulative experiments which employed predator exclusion cages to determine the structuring forces and diversity of benthic communities in two zones along a salinity gradient. I compared Simpson's diversity index and Shannon-Wiener diversity for communities in two salinity zones (5-10 ppt and 15-20 ppt) in the York River (Chapter 2 -I). To validate field caging experiments, I used behavioral observations of the key epibenthic predators, blue crabs, *Callinectes*

*sapidus*, spot, *Leiostomus xanthurus*, croaker, *Micropogonias undulatus*, hogchoker, *Trincects maculatus*, and summer flounder, *Paralichthys dentatus* around cages in a laboratory mesocosm. I also used carbon, nitrogen and sediment analysis to look at differential deposition in varying cages to reveal any caging artifacts and looked at sediment carbon content between two estuarine zones to get an indication of possible "bottom up" (i.e., nutrient) limitation of the benthic communities (Chapter 2-II). Then, I quantified the shallow-water predator guild which preys upon the benthic prey assemblage to determine if differences in predator abundance were responsible for any differences between zones seen in caging experiments. Trawling was conducted around the cages in both downriver and upriver zones (Chapter 2 - III) throughout three months in the summer. Finally, I determined the effect of predation on thin-shelled clams, *Macoma balthica*, in differing salinity zones and assessed the validity of the MS consumer stress model in this marine soft-bottom system. *Macoma balthica* typically shows higher abundances upriver than downriver, and I addressed the hypothesis that the differential distribution was due to higher predation downriver (Chapter 3). I conclude that this system is not driven purely by predation but also by species limitations due to the estuarine salinity regime, and possibly by nutrients and productivity. The York River system may be driven by both "top down" and "bottom up" forces, such as primary production, predation and environmental factors.

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## ABSTRACT

A unifying theory of community regulation in soft-bottom systems remains elusive, despite extensive field studies on the factors controlling community structure. In this investigation, I have (1) reviewed models of community regulation, (2) examined the role of predation in controlling benthic diversity in two zones along a salinity gradient, (3) examined effects of predation upon an abundant bivalve, *Macoma balthica*, and (4) investigated and revised a model of community regulation in an estuarine soft-bottom system. The Menge and Sutherland (MS) model of community regulation was developed for rocky intertidal habitats, but can be modified for soft-bottom systems. This "consumer stress model" posits that mobile consumers feed ineffectively in harsh environments, and that the relative importance of physical disturbance, competition and predation varies predictably with the magnitude of recruitment, environmental conditions, and trophic position. In this model, competition for a resource depends directly upon the level of recruitment, and does not address the joint effects of recruitment and resource availability, which are important in soft-bottom communities. I have revised the model to fit soft-bottom systems by changing the recruitment axis to a "recruitment: resource ratio." Hence, the impact of a given level of recruitment depends upon resource availability, which characterizes different benthic systems.

According to the predictions of the MS model, under extreme environmental stress, physical factors are most important in determining community structure; predation becomes significant when environmental conditions are less severe. Thus, the low diversity in physically stressful habitats results from a reduction in the importance and intensity of predation; in contrast, benign habitats are characterized by high diversity due to an increase in the importance and intensity of predation. In this series of field experiments, I tested the applicability of the MS model in a soft-bottom estuarine community. I quantified predator abundance, prey abundance and diversity, and the differential effect of predation on species diversity and survival of an abundant prey species, *Macoma balthica*, along an estuarine gradient in two tributaries of Chesapeake Bay. Benthic diversity was lower in upriver high-stress habitats than downriver low-stress habitats, in agreement with predictions of the MS model. However, the following findings are inconsistent with model predictions: (1) predator abundance was greater upriver, (2) predation intensity and its impact on benthic diversity were greater upriver, (3) predation-induced mortality of transplanted *Macoma balthica* clams, and natural mortality of clams were higher upriver, and (4) predator removal or enhancement had significant effects on diversity upriver and not downriver. Therefore an alternative community regulation model applies to this system. Higher stress upriver neither inhibited predators from entering that zone, nor from feeding at higher rates. The pattern in predator abundance and predation intensity (higher in zones of higher environmental stress) was contrary to the MS model

predictions. Predators aggregated upriver where carbon production was increased, and prey were abundant. Hence, a more suitable model for this soft-bottom system may be one that incorporates the effects of production and predation along with recruitment, competition and environmental stress.

# EPIBENTHIC PREDATION IN MARINE SOFT-BOTTOM COMMUNITIES ALONG AN ESTUARINE GRADIENT

# *CHAPTER 1:*

# *REGULATION OF MARINE BENTHIC COMMUNITY STRUCTURE : MODELS AND APPLICATION TO CHESAPEAKE BAY*

## *I. FORCES STRUCTURING COMMUNITIES*

Community ecologists seek to characterize patterns in abundance and distribution of species, the key interactions between these species and the relative importance of physical and biological processes to community regulation. These structuring forces include both physical factors (i.e., stressors that exceed a species' physiological tolerance), as well as biological processes (e.g., competition, predation and recruitment; Menge and Sutherland 1987). Although the importance of biological processes in community organization has been documented and modeled for terrestrial and marine hard-bottom and coral reef communities (Hairston et al. 1960, Connell 1961a, b, Paine 1966, Dayton 1971, Menge 1974, Gaines and Roughgarden 1985, Underwood and Fairweather 1989), predation patterns have not been incorporated into a model of community regulation for soft-bottom marine communities, which differ substantially from other marine communities (Wilson 1991). Physical factors also affect benthic communities significantly (Moore 1972, Rosenberg 1977, Alongi 1990, Warwick and Clarke 1993) and must be incorporated into models of community structure (i.e., Menge and Sutherland 1976, 1987). In this review, I sought to elucidate the role of biological interactions and physical stress in regulating all marine benthic communities in both soft and hard substrates and incorporate this information into a revised model for community regulation.

**Experiments on predation and competition**

An understanding of potentially important forces structuring communities arises from reviewing previous investigations in marine systems. Connell and Paine's early work (Connell 1961a, b, Paine 1966, 1969), as well as subsequent studies (Paine 1971, Dayton 1971, Menge 1974) elucidated the fundamental importance of competition and predation in structuring intertidal communities. From this series of investigations, the keystone predator theory was developed. "Keystone" predators control the abundance of competing prey species, preventing competitive exclusion and increasing diversity one trophic level below the keystone predator (Paine 1966). Additionally, predators have a large impact on communities in other systems such as pelagic (see review in Sih et al. 1985), or soft bottom areas (see reviews in Wilson 1991, Olafsson et al. 1994).

Though clear patterns are hard to identify in most systems (Underwood and Denley 1984), investigations in both fresh water and marine soft-sediment habitats have shown some consistent patterns (Hayne and Ball 1956, Peterson 1977, 1979b, Reise 1977, 1985, Virnstein 1977, 1979, Berge and Valderhaug 1983). Soft-bottom systems consistently lack a single keystone predator and competitive dominant. Instead, they have guilds of generalist predators and a complex array of competitive interactions (Hines et al. 1990). Species diversity either remains unchanged or increases when epibenthic predators are excluded in field experiments (Virnstein 1979, Hines et al 1990, Wilson 1991, Olafsson et al. 1994), confirming the absence of a keystone predator or competitive exclusion since diversity does not decrease with predator exclusion (typical of rocky intertidal experiments; e.g., Paine 1966). Applicability of the keystone predator theory

may be limited to selected habitats where immobile, space-limited species are common (Wilson 1991).

In the 100 or more predation experiments in soft sediments, contradictory findings regarding predator effects on infaunal prey abundance and diversity can sometimes be explained by indirect effects. In some investigations, abundance and species richness increased with predator exclusion (Commito 1976, Virnstein 1977, 1979, Reise 1977, 1978, 1985, Bell and Coull 1978, Peterson 1979b, Woodin 1981, Botton 1984); whereas in other instances, the effects of predation were minimal (Berg and Hesthagen 1981, Thorp and Bergey 1981, Choat and Kingett 1982, Ward and Fitzgerald 1983, Raffaelli and Milne 1987, Jaquet and Raffaelli 1989, Mattila et al. 1990, Bonsdorff et al. 1986, Mattila and Bonsdorff 1989). Only epibenthic predators were excluded during these experiments, releasing infaunal predators from predation and allowing them to increase in abundance, reducing abundances of their prey (Ambrose 1984, Commito 1982, Menge 1995).

Soft-sediment communities differ substantially from hard substrate communities, thus the keystone predator or Menge and Sutherland (1987) theories do not necessarily apply directly. Soft-sediment communities are primarily composed of small infaunal species which have an intimate relationship with their habitat -- "they eat it, they lick it, they move through it," and they modify it in many ways (p. 188, Dayton 1984). Hence, many physical, geological and biological process in muddy-bottom estuaries are impacted by the activities of benthic infauna (Day et al. 1989). The three-dimensional nature of soft sediments may allow a refuge from predation and an associated reduction in prey encounter rate when contrasted with that in a two-dimensional habitat (Peterson 1979b).

Competition and recruitment may not have as much influence upon community structure as predation and environmental stress in soft-bottom habitats, because of the three-dimensional nature of the sediment, which promotes coexistence of species (Peterson 1979b). In a recent review, Olafsson et al. (1994) conclude that recruitment limitation is not the dominant determinant of spatial and temporal patterns in soft-bottom systems. The effect of elevated recruitment (typically associated with increased competition) may be minimal, since there is not a decrease in an available resource, due to the three-dimensional nature of the living space and apparent abundance of food (Peterson 1979b). Thus, recruitment does not act similarly in hard and soft-bottom systems and may increase competition only in hard-bottom systems (Olafsson et al. 1994).

**Environmental stress gradients**

Effects of biological factors can be modified by the physical environment (Menge 1974, Menge and Lubchenco 1980, Gilinsky 1984, Cody and Diamond 1975, Menge and Sutherland 1987). Stress can be considered the response of an organism to variation in environmental conditions that are less than optimal for growth, reproduction or survival. Effects depend on how severe and how often conditions deviate from optimal. Environmental stress gradients are caused by both mechanical forces, i.e., "physical stresses" (e.g., air, water, snow, ice, sediments, rocks, logs) and by effects of biochemical reactions, i.e., "physiological stresses" (e.g., temperature, dessication, light, salinity; Menge and Sutherland 1987). Organisms may have an optimal level of each factor, and suboptimal levels can cause minor or lethal damage to the organism (Denny et al. 1985).

The physical environment can be effective in structuring the community, as evidenced by investigations dealing with many different trophic levels (Brett 1970, Thistle 1981, Pihl 1986).

Salinity in an estuary can be used as a surrogate measure of an environmental stress gradient (Menge and Olson 1990), and predator-prey dynamics can be investigated along an estuarine salinity gradient (Hines et al. 1990, Virnstein et al. 1984). Upriver, low-salinity areas experience more severe changes in salinity, temperature and turbidity (Rennie and Nielson 1991), thereby posing a physiologically challenging environment for predators or prey. Shallow temperate brackish areas are characterized by great seasonal variation in abiotic factors (Thorman 1986); periods of intense rain in spring and elevated temperatures in summer cause dramatic declines in salinity and increases in temperature which are most abrupt in upriver areas. Consequently, the consumer stress model of Menge and Sutherland (1987), which posits that predation intensity is inversely related to environmental stress, would predict that physiologically stressful upriver sites will be characterized by decreased importance of predation in controlling community structure, in contrast to less stressful downriver sites. There are no documented tests of the MS model (1987), however, in soft-bottom habitats.

**Summary of important regulating forces in soft-bottom communities**

Experiments in shallow tidal soft-bottom systems are common and the importance of biotic regulating forces to these systems has been reviewed (Peterson 1979b, Schoener 1983, Commito and Ambrose 1985, Reise 1985, Olafsson et al. 1994). In summary,

biological factors can control soft-bottom benthic community structure, though the role of physical factors acting in concert with biological factors needs further investigation. Predation can often reduce species abundance and is thus often an important structuring force, whereas interspecific competition is often unimportant to community structure in soft-bottoms. The impact of biological processes that structure soft-bottom systems may be modified by environmental stress (Menge and Sutherland 1987). Physical stress is important in hard-bottom marine habitats (Menge and Sutherland 1987), and is prevalent in soft-bottom systems (Boesch 1977, Bonsdorff 1989, Mattila 1992), but the influence of environmental stress on the importance of biological factors remains unclear.

Severe stress is likely to reduce the importance of interspecific interactions, such as predation or competition, on influencing community structure (Paine 1966, Menge and Sutherland 1976). Shallow areas are characterized by great seasonal variation in abiotic factors, such as temperature and wave action (Boesch 1977, Rennie and Nielson 1991, Mattila 1992), thus physiological stress may play an important role in community regulation in shallow systems such as tributaries to Chesapeake Bay. I hypothesize that stress is important in structuring soft-bottom systems on a local scale, though physical disturbance may not be as intense in subtidal communities in Chesapeake Bay as on an exposed rocky shore. Processes including gradients in environmental production as well as local stress will influence overall diversity and species distribution.

Unifying theories of community regulation have been developed for hard-bottom systems and thus provide useful heuristic tools for defining important structuring forces in soft sediments. For instance, the importance of predation as a structuring force first

increases and subsequently declines as environmental stress or disturbance in hard-bottom systems increases (Menge 1976, Menge and Lubchenco 1981, Gilinsky 1984, Menge and Sutherland 1987); similar patterns may hold for soft-bottom systems. Perhaps the best approach to utilizing information from localized studies and broadening their applicability is to incorporate their findings using theoretical models that encompass broader spatial and temporal scales, and consequently, a greater range of variation in key biological and physical processes.

## *II. THEORETICAL MODELS*

### Summary of competition and predation models

Conceptual models and empirical evidence may be useful in either explaining or predicting patterns in community structure (i.e., species diversity and abundance) in marine systems. Stochastic variation, such as that from recruitment dynamics, may, however, limit our predictive capabilities (Underwood and Denley 1984). To understand the roles of biotic and environmental forces in structuring benthic communities, we must develop a predictive and explanatory theoretical framework. Fundamental empirical gaps in our knowledge of the effects of competition and predation on the structure of soft-sediment communities have precluded a unifying theory regarding patterns and processes in marine communities. Theoretical models from hard-bottom communities may, however, provide guidance (Menge and Olson 1990).

Theories on community regulation, originally developed in hard-bottom systems,

have emphasized the importance of predation (Paine 1966, Bayne 1981, Connell 1983, Menge and Sutherland 1976, 1987, Glasser 1978, 1979, Oksanen et al. 1981, Schoener 1982, Menge and Olson 1990). The early models of community structure were developed for terrestrial systems (Hairston et al. 1960) and suggested that competitive exclusion occurs only in the absence of predation. In food chains with two levels (i.e., grazers feed upon primary producers), primary producers are regulated by predation. Primary producers do not suffer interspecific competition because grazers regulate their abundance. In food chains with three levels (i.e., carnivores feed on grazers which feed on primary producers), grazer abundance is controlled by carnivores, thus primary producers compete interspecifically. Thus, predator and prey are regulated by different factors (Oksanen et al. 1981). Top carnivores are likely resource limited, whereas plants are controlled by grazers in two-level food chains and by interspecific competition for resources in three-level systems. Thus, the importance of structuring forces differs depending on trophic complexity and linkages, and must be evaluated separately for each community.

The relative impact of competition, predation and physical disturbance as major regulating forces in rocky intertidal communities (Connell 1961a, b, Paine 1966, Dayton 1971) contrasts with results from experiments in marine soft sediments (Woodin 1974, Reise 1977, Peterson 1979b). In soft sediments, processes involving competition, such as trophic group ammensalism and adult-larval interactions (Rhoads and Young 1970, Woodin 1976, 1978, Peterson and Andre 1980), are difficult to demonstrate and may only be important at extremely high infaunal densities.

In soft-sediment habitats, there is little evidence that space is limiting (i.e., interference competition; Woodin 1974, Roe 1975, Peterson and Andre 1980, Levin 1981, Paine 1984, Tamaki 1985, see review in Wilson 1991). Infauna of soft-sediments can penetrate into the sediment and often live amongst one another (Levinton 1977); vertical partitioning of the space is possible, reducing the likelihood of competitive encounters (Wilson 1991). Rhoads and Young (1970) pointed out that functional groups can be mutually exclusive to settlement. For instance, the trophic group ammensalism theory hold that deposit feeders may inhibit settlement of suspension feeders by disturbing and resuspending sediment, thereby clogging the feeding apparatus of suspension feeders.

Food may be a limiting resource in soft sediments. There is evidence for food as a limiting resource to secondary production (i.e., exploitative competition; Peterson and Andre 1980, Peterson 1982, Dauer et al. 1982, Wiltse et al. 1984, Peterson and Black 1987, Olafsson 1988, see review in Olafsson et al. 1994), however, few studies detected impacts of food manipulation on survival. Thus, evidence for strong effects of competition in soft-bottom systems is mixed, and both interference and exploitative competition are of little importance (Peterson 1979b, Olafsson et al. 1994). Extensive reviews have shown agreement that competition is not very important in controlling soft-bottom community structure (Wilson 1991, Olafsson et al. 1994), however, predation has emerged as a major controlling factor (see review in Olafsson et al. 1994).

The influence of predation upon community structure varies by the intensity of predation (Virnstein 1977, Reise 1985, Menge and Sutherland 1987). In the rocky intertidal zone, high local diversity is often maintained by moderate to high levels of

predation, whereby selective predation on dominant competitors prevents competitive dominants from monopolizing food or space (Paine 1966, 1971, 1974). The "intermediate disturbance" hypothesis states that species diversity is highest at intermediate levels of predation (Connell 1978). Predation acts to increase diversity by (1) reducing the density of competitive dominants allowing competitively inferior species to increase, (2) reducing most species densities to a level below that regulated by competitive exclusion, and (3) creating patches with lower densities at different stages of succession to hypothetical climax communities (Paine 1966, 1971, Virnstein 1977, Reise 1985, Mattila 1992). Extremely high predation pressure, alternatively, may decrease diversity by causing local extinctions of relatively rare species. Therefore, predation can potentially enhance or reduce species diversity, depending on its intensity.

Intertidal hard-bottom communities are easily manipulated and have been extensively studied, yielding a synthetic model of community regulation (Menge and Sutherland 1976). In this model, competition and predation act in concert such that competition is more important at higher trophic levels, while predation maintains diversity at lower trophic levels (Menge and Sutherland 1976, Dill 1987). In addition, the relative importance of predation increases in trophically complex systems.

Further development of a community structure model includes the effects of competition, predation and recruitment along gradients of disturbance or stress (Menge and Sutherland 1987). This "consumer stress model" posits that mobile consumers are excluded from, or feed ineffectively in, harsh environments, and that the relative importance of physical disturbance or physiological stress, competition and predation

varies predictably with the magnitude of recruitment (Menge 1991), environmental conditions, and trophic position (Menge and Olson 1990). Under extreme environmental stress, physical factors are most important in determining community structure; predation becomes significant when environmental conditions are less severe. Furthermore, expanded models incorporate small-scale regulatory factors (e.g., competition, predation and physical disturbance) as well as large-scale factors such as environmental stress, productivity, and energy production by plants (Menge and Olson 1990). In sum, the model predicts that at low environmental stress, predation is important, and at high recruitment and intermediate environmental stress and predation, competition is most important.

**Environmental stress models (ESMs)**

The effect of environmental stress on an organism can be either direct (e.g. temperature, salinity, moisture, and light) or indirect and, as such, is influential upon community structure (Menge and Sutherland 1976, 1987, Menge and Olson 1990). Models incorporating gradients in environmental stress in marine systems are replete for the rocky intertidal habitat (Menge 1976, Menge and Sutherland 1976, Menge and Farrell 1989, Denny et al. 1985). These ESMs predict that the influence of species interactions on community structure depends directly on the degree of environmental stress (Menge and Olson 1990). Furthermore, trophic complexity depends upon environmental stress; for instance, food chain length should increase under benign environmental conditions.

Moreover, the specific outcome of stress depends on whether predators or prey are more affected, thereby yielding either prey stress models or consumer stress models.

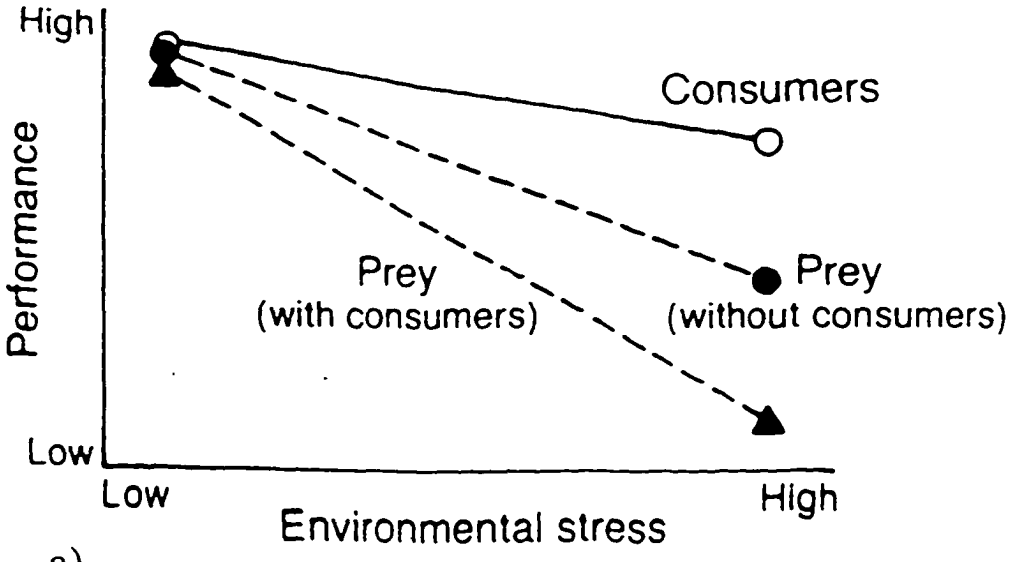
- **Prey stress models (PSMs)**

In PSMs, prey species are more severely affected by environmental stress than predators, such that prey defenses are weakened more than the consumer's activity (Fig. 1.1a; Menge and Olson 1990). At low environmental stress levels, predators and prey are equally affected, but at increased stress, the activity of predators is little reduced, but that of prey falls markedly. This predicts that consumers would be highly active and effective at high environmental stress, thereby increasing the importance of predation and reducing diversity. These models are hypothesized to apply to plant control by herbivores.

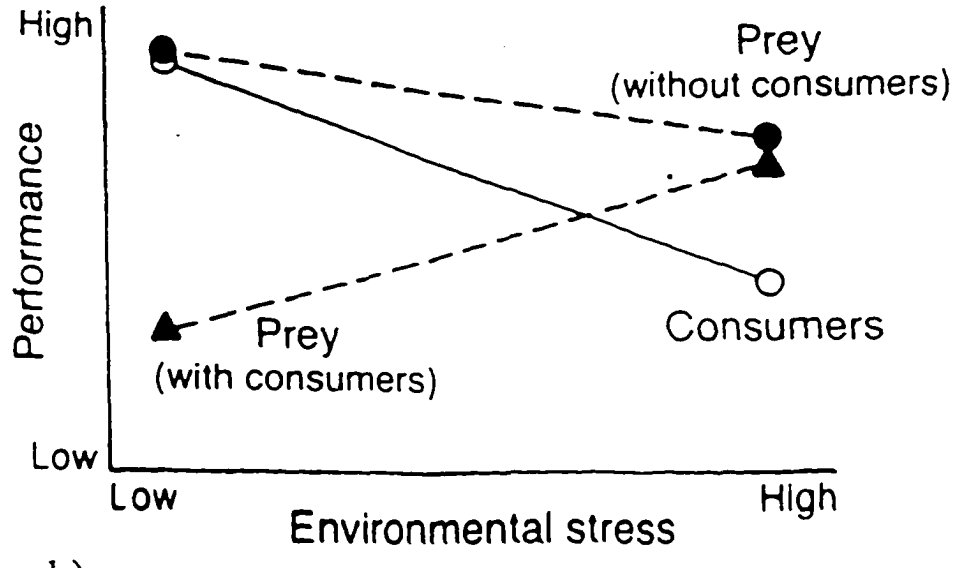
- **Consumer stress models (CSMs)**

CSMs are those that assume the consumer is more severely affected by environmental stress than the prey (Fig. 1.1b). In high stress environments, predators are inhibited, and prey abundance is predicted to increase, consequently increasing interspecific competition. Under low stress, predation intensity is high, and prey abundances are controlled by predators, thereby reducing competition (Menge and Olson 1990). Depending on the level of competition, infaunal species diversity could be enhanced or reduced at low environmental stress, i.e., enhanced if there is no competitive dominant, or reduced if there is a competitive dominant.

Fig. 1.1. Contrasting predictions of alternative environmental stress models. (a). In prey stress models, prey (dashed lines) are expected to be more severely inhibited by increasing stress than consumers (solid lines). Performance in prey decreases at high environmental stress without consumers present (solid circles), and decreases more severely with consumers (solid triangles). As a result, the effect of consumers on prey increases with increasing stress. (b). In consumer stress models, consumers are expected to be more severely inhibited by increasing stress than are prey. The performance of consumers decreases markedly at high environmental stress (open circles), releasing prey from consumers, thereby increasing prey performance at high stress (solid triangles). Thus, the relative effect of consumers on prey decreases with increasing stress. (Modified from Menge and Olson 1990).




a).



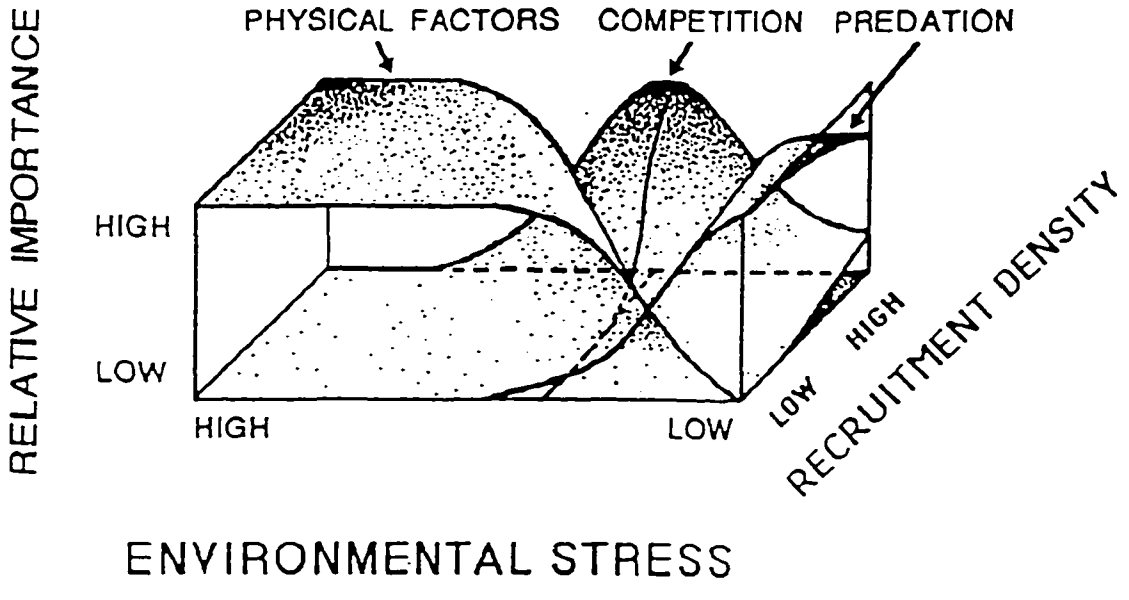

b).

A corollary of this model states that where an environment is "severe" and "unpredictable," adaptations are to the physical environment, but in "benign" or "predictable" environments, adaptations are to other organisms and the community is controlled biologically (Sanders 1969). The latter situation may characterize downriver, high-salinity habitats of Chesapeake Bay, where physical conditions are not rigorous. If a consumer stress model can apply to these systems, and if downriver habitats are biologically controlled, the importance of predation should be greater there than in areas with more severe physical conditions (i.e., upriver).

- **Recruitment models**

The most recent model of Menge and Sutherland (1987), hereafter referred to as the MS model, incorporates recruitment density (influx of new individuals into the population) into the environmental stress model (Fig. 1.2). The level of recruitment alters the importance of competition and predation; often, at low recruitment, competition is reduced (Gaines and Roughgarden 1985, Underwood and Fairweather 1989). In the two-dimensional rocky intertidal system, where space is limiting, higher recruitment exacerbates competition for that limiting resource. The effect of recruitment limitation on community structure in soft sediments has only recently been addressed (Summerson and Peterson 1984, Peterson 1991, Peterson and Summerson 1992). A comprehensive review concluded that recruitment limitation does not appear to determine spatial and temporal patterns in soft-sediment systems (Olafsson et al. 1994).

Fig. 1.2. Model of community regulation at intermediate trophic level (i.e., first consumers), showing the predicted relative importance of (i.e., the proportion of community variance caused by) disturbance (physical factors), competition, and predation (consumption) in relation to variation in environmental stress and recruitment density and/or growth rates of recruits; modified from Menge and Sutherland (1987).



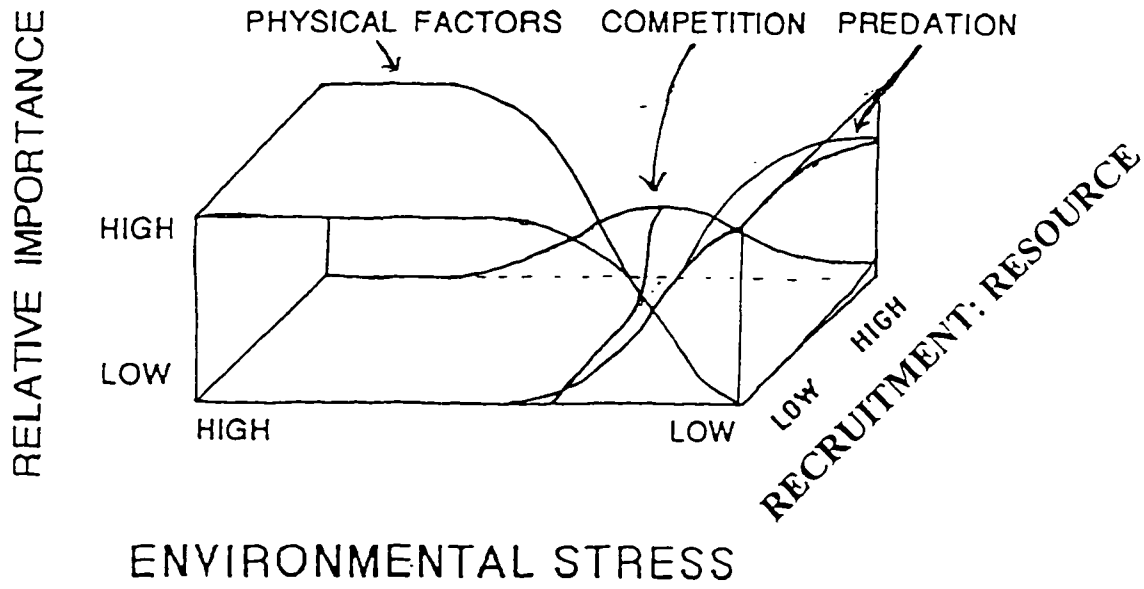
**Nutrient/Productivity models (N/PMs)**

N/PMs have been developed for various systems with low productivity (Fretwell 1977, Oksanen et al. 1981). In these models, plants in relatively unproductive systems do not produce enough energy to support the herbivores in the community, there are many basal (i.e., plant) species, and the community is thereby controlled by interspecific competition. In more productive systems, energy is sufficient to support both herbivores and carnivores, consequently increasing the importance of predation in community regulation. In this case, nutrient or productivity levels determine trophic complexity rather than environmental stress (Menge and Olson 1990). Though there is evidence for food limitation in both deposit- and suspension-feeders (see review in Olafsson et al. 1994), the effects are often on growth and fecundity, whereas effects on survival are rare.

## *III. REVISED MODEL OF MARINE BENTHIC COMMUNITY REGULATION*

Previous theoretical models provide a framework for development of a community regulation model that incorporates soft-sediment communities, which formerly eluded a unifying theory (Wilson 1991). The MS model, developed from, and applied to, the rocky intertidal zone, can be modified to apply to other habitats, such as soft sediments. The MS model does not consider soft-sediments nor does it recognize that soft-sediment

Fig. 1.3. Model of community regulation for soft-bottom systems at intermediate trophic level, showing the predicted relative importance of physical factors, competition, and predation in relation to variation in environmental stress and the recruitment: resource ratio (the relative amount of recruitment to available space or food). In this model, the effect of competition is minimal along the majority of the recruitment: resource axis and only becomes important at extremely high recruitment: resource ratios. (Modified from Menge and Sutherland 1987). This differs from Fig. 1.2 in that even at high recruitment in soft bottoms, the importance of competition is never as great as in areas of high recruitment in hard bottoms.



habitats may have recruitment densities that equal those of hard-bottom, space-limited habitats, without competition becoming important.

In this modification, I consider the differential importance of competition in systems with differing resource availability. The recruitment axis of the MS model is revised to include the three-dimensional nature of soft-sediments by relating recruitment to resource availability. In this modified model, the recruitment axis is changed to a "recruitment: resource ratio" (Fig. 1.3) wherein the impact of a given level of recruitment depends upon resource availability. For instance, when recruitment and resource availability are relatively low, or when recruitment and resources are comparably high, then a low recruitment: resource ratio applies, and competition does not strongly impact community structure. In soft sediments (or presumably other habitats) where the resource (e.g., space) is abundant, a high recruitment may be associated with a extensive available settlement habitat (i.e., resource) and the system would have a *low* "recruitment: resource ratio." Hence, this level of recruitment: resource ratio leaves the system at the front face of the model (Fig. 1.3), which suggests little influence of competition; this is consistent with scant evidence for competition in soft-sediment habitats (Dauer et al. 1982, Wiltse et al. 1984, Wilson 1991). Though more common in space-limited hard-bottom habitats, there may be an extremely high level of recruitment in soft-sediment communities where resources, either food or space, become limiting and competition becomes influential (see review in Wilson 1991). In this situation, the recruitment: resource ratio is *high*, bringing

the system to the back face of the model (Fig. 1.3) where interspecific competition is somewhat important. Along the environmental gradient, the predictions are similar to those set forth in the MS model for a given recruitment: resource ratio. For example, at low recruitment: resource ratios and relatively benign environmental conditions, the importance of predation is greater than at high environmental stress, where physical factors dominate and the importance of predation is reduced (Figs. 1.2 and 1.3).

The relative importance of structuring forces on species diversity are similarly modified from the MS model for species diversity (Fig. 1.4; Modified from Menge and Sutherland 1987). In the MS diversity model, developed for hard-bottom systems, when recruitment is high, the diversity curve is bimodal, with low diversity due to competitive exclusion at the midpoint. When recruitment is low, competition among prey is not important, resulting in a unimodal curve (as in the front face of Fig. 1.2). The important missing component of the MS model is a recognition of systems that are not limited by resources, and, thus, are able to absorb a high recruitment without increased competition (Fig. 1.5).

In soft-bottom systems, when recruitment is relatively low, the predictions for benthic diversity are the same as those for hard-bottom systems, i.e., competition among prey is not important, and diversity increases until predation becomes severe enough to cause local extinctions. However, at high recruitment, resources are still not limiting and the effect of competition will not be as great as in hard-bottom systems. Competition may be moderately important, leading to exclusion, reducing diversity, and causing a bimodal diversity curve (Fig. 1.5) with a less severe dip than in hard-bottoms (Fig. 1.4).

Fig. 1.4. Remake of Menge and Sutherland's (1987) synthetic model of species diversity which is derived mainly from rocky intertidal data. When recruitment is high and competition leads to exclusion, the diversity curve is bimodal. The left mode of the diversity curve is the intermediate (physical)-disturbance model and the right mode is the predation model of species diversity. When a broad range of physical conditions is considered, this bimodal curve predicts the changes expected in species diversity as physical conditions ameliorate. When recruitment is low, competition among prey is not important (as in Fig. 1.2), and species diversity depends on the interaction among the physical environment, predation intensity, and colonization patterns. If we assume that the number of locally competent species that can successfully colonize and persist increases with decreasing stress, diversity should increase until predation becomes severe enough to cause local extinctions. The result should be a unimodal curve.

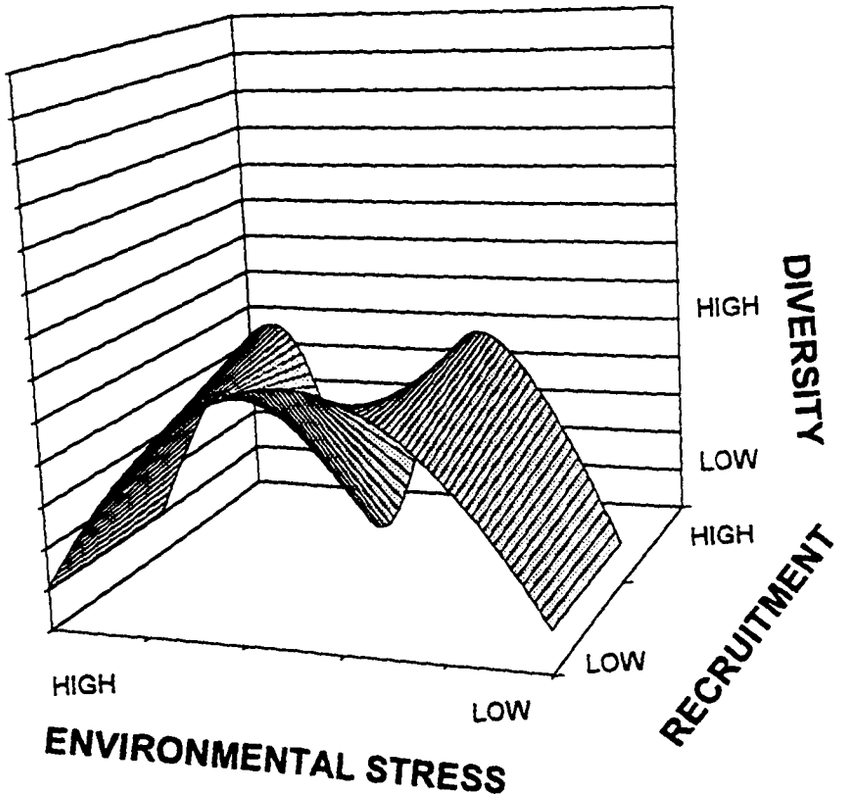
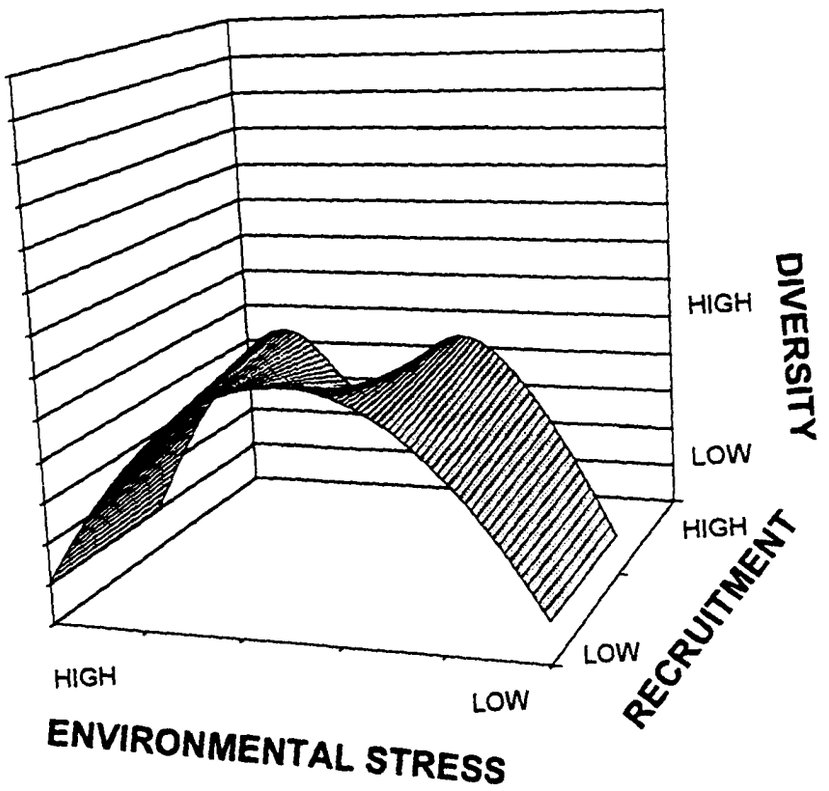


Fig. 1.5. Model of species diversity in soft-bottom systems. When recruitment is low, competition among prey is not important, as in hard-bottom systems (see Fig. 1.3). At this point, species diversity depends on the interaction among the physical environment, predation intensity, and colonization patterns. The result is a unimodal curve with diversity increasing until predation becomes severe enough to cause local extinctions. However, at extremely high recruitment, resources may be slightly limiting and the effect of competition will not be as great as in hard-bottom systems. If competition is important, it may lead to exclusion, reducing diversity, and causing a bimodal diversity curve with a less severe dip than that predicted for hard-bottom systems (Fig. 1.4). (Modified from Menge and Sutherland 1987).



To apply the MS diversity model to soft-bottom as well as hard- bottom systems, it is helpful to conceptualize variation in the importance of competition with resource availability across recruitment values for these different systems (Fig. 1.6). When recruitment is low, the importance of competition is necessarily low throughout a range of systems with differing magnitudes of resource availability. When recruitment is high, and available resources are high (as is typical in three-dimensional soft-bottom systems; the front face of the model, Fig. 1.6), the importance of competition rises slowly to an upper asymptote. When recruitment is high and available resources are low (such as limited space in hard-bottom systems; the back face of the model, Fig. 1.6), the importance of competition rises quickly to an upper asymptote well above that seen for high resource availability (i.e., in soft bottom systems). The overall effect is a reduced importance of competition in areas with high resource availability.

I modify the MS diversity model to allow application of the model to soft sediments and any benthic system by changing the recruitment axis to a recruitment: resource ratio (Fig. 1.7). At high environmental stress, the new model, like the MS model, predicts that physical factors will limit species diversity, whereas at intermediate environmental stress, the importance of both physical factors and predation will be minimal, leading to increased diversity, as in the MS model at low recruitment (Fig. 1.2). Finally, as in the MS model, In more benign environments, the importance of predation increases, thereby decreasing diversity. Because of low recruitment, competition should not be important. Thus, at low recruitment: resource ratios, a unimodal curve of species diversity applies. Typically in soft-bottom systems, resources are not limiting, the

Fig. 1.6. Conceptual model of variation in the importance of competition with resource availability across recruitment values for a range benthic systems. When recruitment is low, the importance of competition is necessarily low, with any magnitude of resource availability. When recruitment is high, and available resources are high (as is typical in three-dimensional soft-bottom systems), the importance of competition rises slowly to an upper asymptote. When recruitment is high and available resources are low (such as limited space in hard-bottom systems), the importance of competition rises quickly to an upper asymptote well above that seen for high resource availability (i.e., in soft bottom systems). The overall effect is a reduced importance of competition in areas with high resource availability.

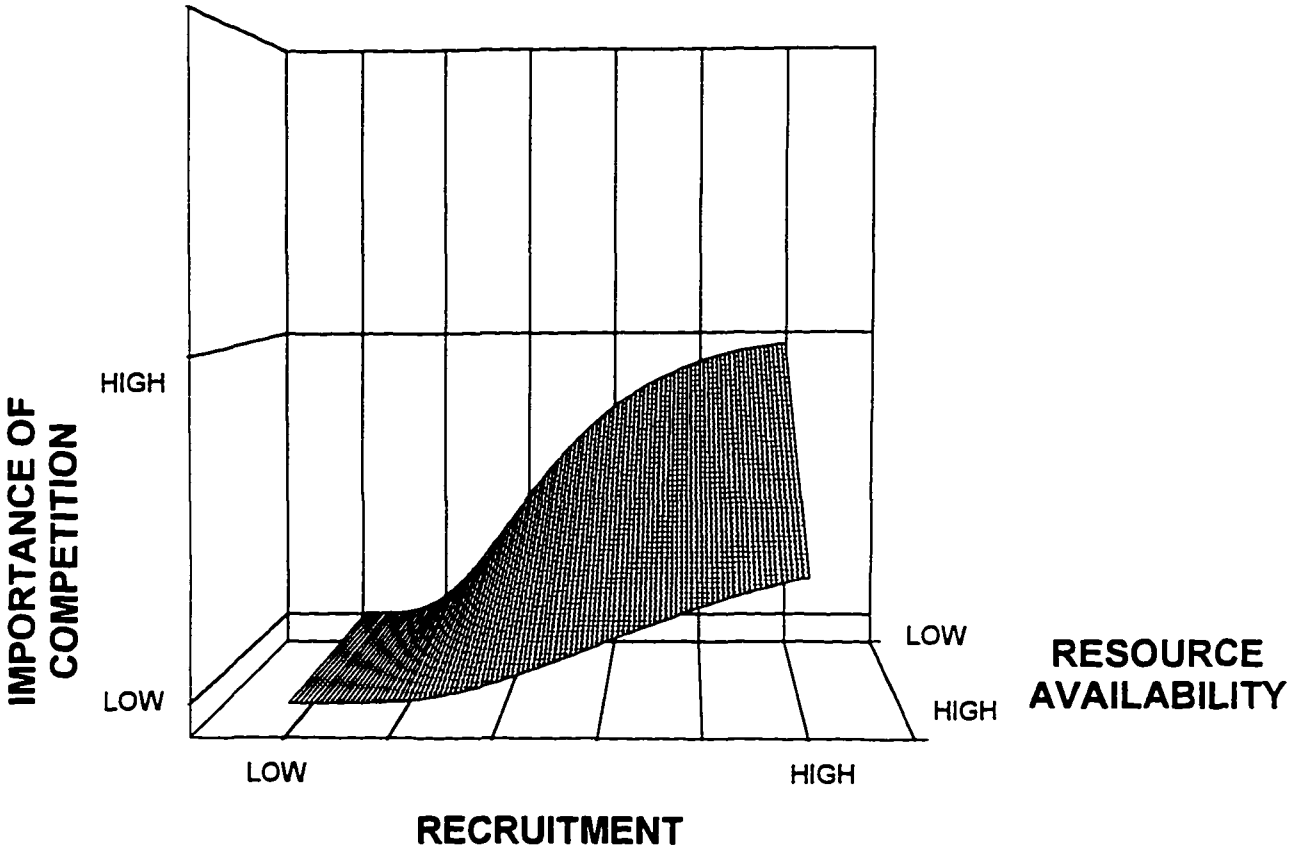
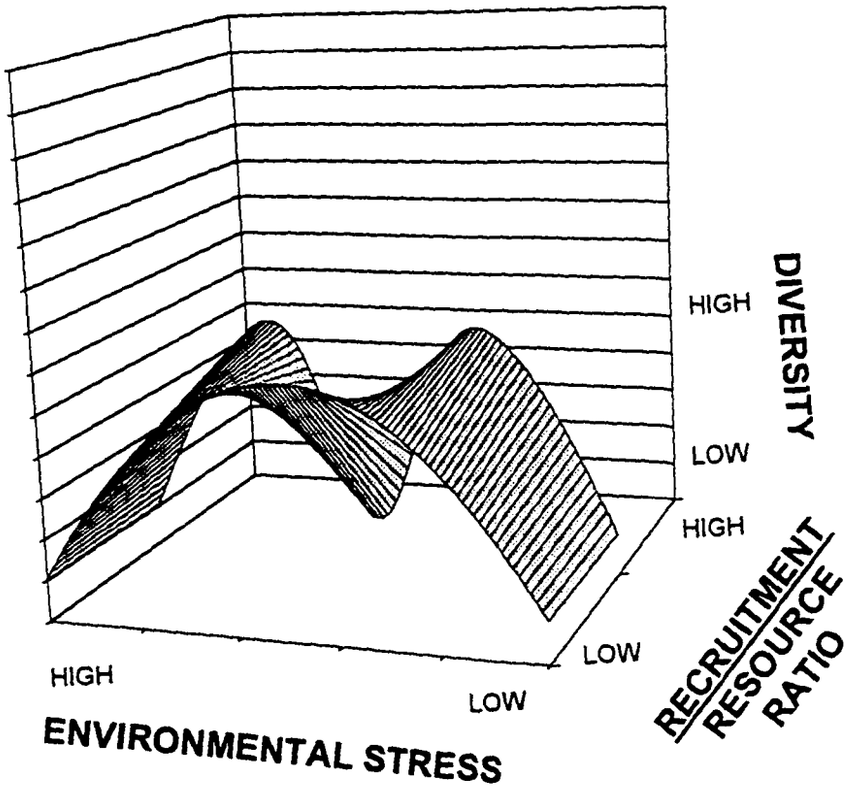


Fig. 1.7. New modified Menge and Sutherland synthetic model of species diversity in all benthic systems incorporating the recruitment to resource ratio. When recruitment is low, recruitment: resource ratio will be low and competition among prey is not important (see Figs. 1.2 & 1.3), At this point, species diversity depends on the interaction among the physical environment, predation intensity, and colonization patterns. As environmental stress decreases, the number of colonizing species increases, and diversity should increase until predation becomes severe enough to cause local extinctions. The result should be a unimodal curve. However, at extremely high recruitment, when resources may be limiting and the recruitment: resource ratio is high, competition may lead to exclusion, reducing diversity, and causing bimodal diversity curve. Typically in soft-bottom systems, resources are not limiting and the recruitment: resource ratio is low to moderate and the diversity curve would be expected to be mostly unimodal. In hard-bottom systems, resources are more limiting and competition is important, leading to a bimodal diversity curve (Modified from Menge and Sutherland 1987).



recruitment: resource ratio is low to moderate, and the diversity curve would be expected to be unimodal. In contrast, at high recruitment: resource ratios, an uncommon situation for soft-sediments where the three-dimensional space is generally not limiting, species diversity is bimodal (i.e., intense competition may pertain at intermediate environmental stress levels where neither physical factors nor predation are intense). A predicted bimodal diversity curve may characterize hard-bottom systems, where resources are limiting and competition is important. The hypotheses of a unimodal diversity curve in soft-sediment systems and a bimodal one in hard-bottom systems can be rigorously tested.

Hence the modified model of community regulation permits incorporation of a variety of soft-sediment habitats, from the coastal ocean to the deep sea. Its predictions, however, remain to be tested. In the following investigation, I experimentally examine the influence of predation upon benthic community structure along an environmental gradient, and apply the modified MS model of community regulation to the findings.

## *IV. A MODEL SYSTEM*

### The Chesapeake Bay predator-prey system

An understanding of the predators and prey in a given system is necessary for understanding the importance of different structuring forces within that system. In Chesapeake Bay, dominant epibenthic predators include the blue crab, *Callinectes sapidus*, as well as various demersal fishes such as spot, *Leiostomus xanthurus*, and

croaker, *Micropogonias undulatus* (Horwitz 1987, Hines et al. 1990). The benthic prey assemblage is dominated by infaunal polychaetes and bivalves (Boesch 1977, Virnstein 1977, 1979, Holland 1985, Holland et al. 1987, Hines et al. 1990). Secondary production by benthic organisms is the major pathway by which organic carbon is recycled out of the sediment and to higher trophic levels (Diaz and Schaffner 1990). The secondary production in this estuary is high, at approximately 17 g C/$m^2$/yr (Diaz and Schaffner 1990), and a large percentage of the total number of infauna is eaten by epibenthic predators (Virnstein 1977, Holland et al. 1980, Hines et al. 1990, Diaz and Schaffner 1990). In this system, infaunal species are the most important prey for epibenthic piscine and crustacean predators (Virnstein 1979, Hines et al. 1990, Mansour 1992).

The blue crab is dispersed widely along the Atlantic and Gulf coasts of North America, and is abundant throughout Chesapeake Bay (Williams 1984, Hines et al. 1987, 1990, Lipcius and Van Engel 1990). This species is important in energy transfer in estuaries, serving as both omnivore and prey (Baird and Ulanowicz 1989). Feeding efficiency and prey capture in blue crabs vary significantly with prey availability, predator density and habitat complexity (Blundon and Kennedy 1982a, b, Arnold 1984, Lipcius and Hines 1986, West and Williams 1986, Hines et al. 1990, Eggleston 1990, Mansour and Lipcius 1991, Eggleston et al. 1992). The diet of blue crabs, however, consists mainly of bivalve molluscs, predominantly *Mya arenaria* and *Macoma balthica*, and conspecifics, as well as polychaetes, other crabs and fish (Laughlin 1982, Alexander 1986, Hines et al. 1990, Mansour 1992, Ebersole and Kennedy 1995).

Epibenthic fish, *Leiostomus xanthurus* (spot), *Micropogonias undulatus* (croaker), and *Trinectes maculatus* (Hogchoker) were among dominant predators identified in the Rhode River, a Chesapeake Bay tributary (Hines et al. 1990). *Leiostomus xanthurus* populations consisted of a singe size class which migrated into the subestuary in May. This species fed primarily on *Macoma balthica* siphons, small crustaceans and meiofauna. *Micropogonias undulatus* was also composed of a single size class but moved into the estuary in November. This species fed extensively on amphipods and polychaetes. *Trinectes maculatus* was composed of three year classes, was present year-round, and fed on amphipods, polychaetes and clam siphons.

In most shallow-water marine systems, the predatory guild is dominated by generalists capable of consuming a diversity of prey (Virnstein 1977, 1979, Peterson 1979a, b, Levinton 1982, Dayton 1984, Livingston 1984, Hines et al. 1990). Chesapeake Bay is no exception, with mobile generalist predators having overlapping diets of a diversity of prey including polychaetes, small crustaceans and clam siphons (Hines et al. 1990). Though predation is a dominant controlling factor in Chesapeake Bay benthic systems (Virnstein 1979), there is not dominance by a single keystone-type predator since all are generalists (Hines et al. 1990), and competitive exclusion is unlikely (Virnstein 1977, Peterson 1979b). In some cases, when predation is intense, the predator feeds upon a wide range of prey species, causing an associated decline in the entire benthic community (Gilinsky 1984).

In contrast, some rocky intertidal habitats are characterized by competitively dominant prey and a "keystone" predator (Paine 1966). Such predators can affect the

structure of communities and persistence of populations by increasing diversity (Menge and Sutherland 1987, Wilson 1991, Sih et al. 1985), depending on the form of the predator-prey interactions with individual species. Generalist predators therefore can have a negative effect on diversity, in contrast to a keystone predator, which typically maintains high diversity (Paine 1966).

## *V. APPROACH*

Using the Cheasapeake Bay and its tributaries as a model system in which to test the ideas of predator-prey relationships in a soft-sediment habitat, I set forth the following objectives:

- To determine how macrobenthic species diversity and abundance are affected by different predators using various cage designs that exclude specific predators from benthic habitats;
- To determine how an environmental gradient of stress correlated with salinity (i.e., upriver and downriver) modifies the impact of predation on macrobenthic community structure;
- To assess the effects of predator exclusion cages on predator behavior, sediment grain size and nutrient deposition.
- To assess differences in shallow-water predator abundances associated with upriver and downriver areas in the York and Rappahannock Rivers.

- To test the effect of predation on bivalves along a salinity gradient in two replicate systems over the long-term (i.e., two-years) and over short periods (i.e.. weeks) during the summer.

This dissertation will add to our knowledge of the effect of predation on community regulation in soft-bottom habitats, and the modification of the impact of predation by environmental stress.

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# *CHAPTER 2:*

# *THE EFFECT OF EPIBENTHIC PREDATORS ON BENTHIC DIVERSITY ALONG AN ESTUARINE GRADIENT*

*ABSTRACT*

Regulation of benthic community structure has been studied extensively in marine systems, resulting in a community regulation model that incorporates the effect of predation, competition, environmental stress and recruitment - the Menge and Sutherland consumer stress model (MS). This model predicts that low diversity in physically stressful habitats results from a reduction in the importance of predation; in contrast, benign habitats are characterized by high diversity due to an increase in the importance of predation. In this investigation, I have quantified predator abundance, prey abundance and diversity, and the differential effect of predation along an estuarine gradient in tributaries of Chesapeake Bay to examine the applicability of the MS model in a soft-bottom estuarine community. Benthic diversity was lower in upriver higher-stress habitats than downriver lower-stress habitats, in agreement with predictions of the MS model. However, the following findings are inconsistent with predictions from the MS model: (1) predator abundance was greater upriver, and (2) predator removal or enhancement had significant effects upriver and not downriver, and therefore (3) the MS model needs to be modified substantially to be applicable to this system. Higher stress upriver neither inhibited predators from entering that zone, nor from consuming prey. This soft-bottom benthic system is apparently not driven purely by "top-down" forces, but is probably regulated by "bottom-up" forces indicated by increased carbon production upriver and associated increased predator abundance. Thus, the system is regulated by a combination of salinity tolerance, primary production and predation.

# THE EFFECT OF EPIBENTHIC PREDATORS ON BENTHIC DIVERSITY

# *INTRODUCTION*

## *Community structure*

Benthic community structure is driven by both biological (Hairston et al. 1960, Connell 1961a, b, Paine 1966, Dayton 1971, Menge 1974) and physical forces (Moore 1972, Rosenberg 1977, Alongi 1990, Warwick and Clarke 1993), whose impact is well documented for terrestrial and marine hard-bottom communities. Biological forces include predation, competition and recruitment of young. Numerous field experiments manipulating the abundance of predators or competitors (e.g., through the use of predator exclusion cages in the rocky intertidal; Connell 1961a, 1983, Paine 1966, Menge and Sutherland 1976) show the importance of these structuring forces in hard-bottom systems. The keystone predator concept (sensu Paine 1966) has emerged from these studies, whereby such predators enhance species diversity by allowing competitive exclusion. The exclusion of a keystone predator results in the decline of competitively inferior prey species and increase by a competitive dominant, thereby reducing species richness and diversity (Paine 1966, 1974, Peterson 1979b, Menge 1995).

Soft-bottom marine communities differ substantially from other marine communities (Wilson 1991) and structuring forces have not been determined sufficiently in these systems. Soft-bottom systems are ubiquitous in the marine environment, are important for transfer of food through food webs. They also can be productive and

important as feeding grounds, spawning areas and nurseries (Adams 1976, Pihl 1982, 1985, Evans 1983, 1984). These habitats are characterized by high seasonal fluctuations in salinity, temperature, and wave action which have an effect on community regulation along with biotic interactions (Boesch 1977, Mattila 1992).

Biological factors such as predation may or may not control soft-bottom community structure (Connell 1975, Peterson 1977, 1979a, b, Virnstein 1979, Sih et al. 1985, Menge and Farrell 1989, Hines et al. 1990, Thorp 1986, Wilson 1991). In soft-bottom communities, species diversity either increases or remains unchanged when epibenthic predators are excluded (Virnstein 1979, Holland et al. 1980, Hines et al. 1990, Wilson 1991), indicating the absence of both keystone predators and interspecific competition.

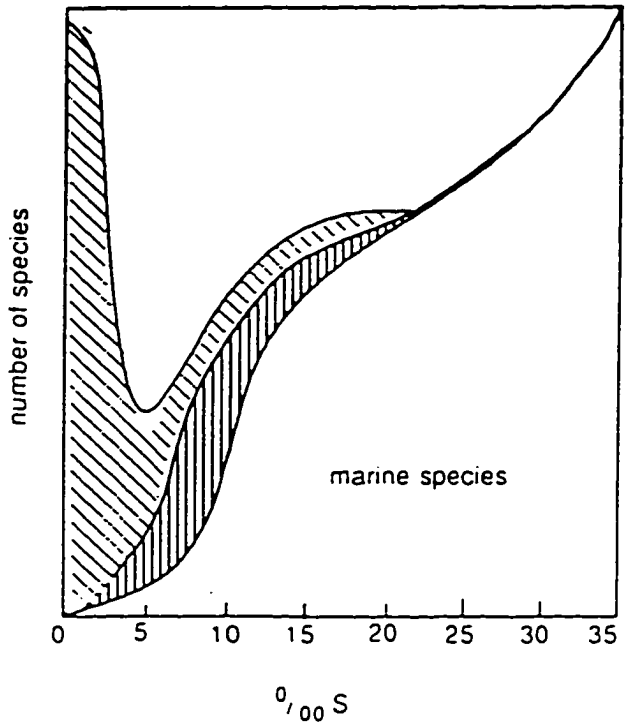
Biological forces can be modified by the physical environment and can change along gradients of environmental stress. The effects of both biological (e.g., predation) and environmental (e.g., stress) structuring forces on benthic community structure, however, have not been satisfactorily determined for marine soft-bottom systems. Species abundance, diversity, food web size, food web complexity, and the major species interactions are often connected with gradients in elevation, water flow or salinity (Boesch 1977, Menge and Olson 1990). For example, species diversity increases with decreasing latitude and with decreasing depth in the deep sea (Jackson 1972, Virnstein et al. 1984, Grassle et al. 1979, Rex et al. 1993). An estuarine gradient may also be important in modifying benthic community structure, and this study addresses the influence of predation along an estuarine salinity gradient within tributaries of Chesapeake Bay.

An environmental gradient in salinity can affect species diversity. For example, in estuaries, diversity increases with salinity due to the marine origin of most species and their consequent inability to cope with reduced or fluctuating salinities (Fig. 2.1; Boesch 1971, Remane and Schlieper 1971, Wolff 1983). Thus, benthic diversity is lower in estuaries, but abundance may be higher due to elevated food availability, among other things (Day et al. 1989). In Chesapeake Bay, benthic infaunal distribution and abundance are associated with salinity gradients in addition to other physical factors such as sediment type, oxygen concentration, and frequency of bottom disturbance (Boesch et al. 1976, Schaffner et al. 1987, Pihl and Rosenberg 1992). This study addresses a community that lies between 5 and 25 ppt, with an upriver, low salinity zone near the minimum in estuarine diversity. The benthic community may be regulated by a suite of biotic and physical or physiological factors, which may be addressed in models of community regulation.

***Community regulation models***

Community regulation has been variously modeled, particularly by environmental stress models, whose predictions depend on whether the prey or consumers are more affected by stress (Menge and Olson 1990). Prey Stress Models (PSMs) predict that stress weakens prey more severely than predators, thus predation has a greater effect in high stress areas. For example in anoxia, benthic fauna may be weakened, rise to the sediment surface, and be eaten by predators that are less severely affected because they can migrate. Conversely, Consumer Stress Models (CSMs) predict that consumers are

Fig. 2.1. Changes in species richness (number of species) along a salinity gradient (from Remane and Schlieper 1971).



more affected by stress than prey, reducing predation, increasing prey abundance, and thereby increasing competition in high stress habitats.

One dominant model for community regulation is the Menge and Sutherland (MS) consumer stress model (1987). This model, which was developed for the rocky intertidal habitat, posits that consumers are more severely affected by environmental stress than prey. Specifically, the MS model suggests that if a consumer stress model applies, the importance of predation increases with reduced environmental stress, because of an increase in predator foraging efficiency in areas of lower stress (Menge and Lubchenco 1981, Gilinsky 1984, Menge and Sutherland 1976, 1987, Menge and Farrell 1989). For instance, in areas of low wave exposure (low stress), the predatory starfish *Pisaster* is common and limits epifaunal prey density; in areas of extreme wave exposure and stress, its foraging activities and impact are minimal (Menge 1975). Such trends in predation over varying levels of environmental stress may also hold for soft-bottom communities (Sih et al. 1985).

A major tenet of the MS model is that diversity increases and the importance of predation increases with a decrease in environmental stress. In addition, the model predicts that low stress environments have low diversity because reduced predator activity allows competitive exclusion. This model was developed for processes on a local scale (e.g., across the intertidal zone) where the suite of predators and prey span the gradient between the two zones and the model may best apply to small spatial scales (Menge and Olson 1990). I will, however, examine the utility of this model on larger spatial scales where the suite of predators is similar, but prey species change substantially across the

gradient of interest, i.e., a soft-bottom system along a salinity gradient in the York and Rappahannock Rivers, Chesapeake Bay.

Environmental stress models (ESMs) may not be applicable to all systems and Nutrient/Productivity models (N/PMs) may be more appropriate in some situations (Menge and Olson 1990). According to the expected domain of ESMs or N/PMs, intertidal areas should be mostly controlled by ESMs at local scales, while N/PMs are predicted to be influential at larger meso- and geographic scales. Shallow waters should be controlled by ESMs while deeper areas should be influenced by N/PMs. Large river and stream systems should be controlled by N/PMs, while small rivers and streams should be controlled by ESMs. In sum, if a given habitat has a high level of environmental stress, it is likely to be influenced by an ESM, whereas if stress is low to moderate, N/PMs may apply better. With these predictions, it is not clear whether a shallow river system spanning a large geographic scale (~20 km) should be influenced by an ESM or N/PM. The York and Rappahannock River systems spanning an estuarine gradient in stress (e.g., salinity, temperature, turbidity), provide a good model for examining the applicability of different community regulation models to a soft-bottom community.

If we assume that interspecific competition is not important in soft-bottom systems (Peterson 1979b, Sih et al 1985, Wilson 1991), then diversity should show a unimodal peak along a gradient of environmental stress (Menge and Sutherland 1987). Diversity increases with decreasing environmental stress, as does the importance of predation in community regulation. Diversity is low at high environmental stress because few benthic species can tolerate extreme physical conditions (Kinne 1970, Boesch 1977). At

intermediate stress, diversity is highest. At low stress, predators become efficient and eliminate some prey species, thereby decreasing diversity. If the MS model can be applied to this system, I predict, in accord with Menge and Sutherland, that the importance of predation should increase with a decrease in environmental stress, along with a consequent increase in diversity. In the case of soft-bottom systems, diversity would not change due to competitive exclusion, but may instead change due to the effect of predators on evenness. Because of the presence of many generalist predators (Hines et al. 1987) that can consume abundant species, evenness may increase with predator abundance.

Species diversity varies at many scales from local to global (Rosenzweig 1995), and often in concert with the intensity of competition, predation, disturbance, and environmental gradients (Paine 1966, Connell 1978, Sih et al. 1985). In Chesapeake Bay, for example, diversity of benthic infauna covaries positively with a gradient in salinity (i.e., higher diversity in more saline waters; Boesch 1977). Patterns in benthic species diversity are related to gradients in environmental conditions in various ecosystems. Stable environmental conditions often result in higher diversity, as in the tropics where fluctuations in temperature and other environmental factors are minimal and diversity is high (Jackson 1972, Virnstein et al. 1984, Rex et al. 1993). For example, tropical forests support 10 times more tree species than temperate forests of equal biomass (Latham and Ricklefs 1993). High salinity zones in estuaries exhibit less fluctuation in abiotic conditions and diversity is increased compared with lower salinity areas (Boesch 1977). The deep sea is more stable than coastal zones and diversity increases with increased depth (Grassle 1989).

In this study, salinity is used as a surrogate measure to define an environmental gradient and test its impact upon predator-prey dynamics in marine soft-bottom systems (Menge and Olson 1990). Variation in the importance of predation has not been investigated along salinity gradients, even though such gradients are a ubiquitous feature of estuaries (Boesch 1971). In general, upriver low-salinity areas experience more extreme fluctuations in salinity, temperature, and turbidity than downriver high-salinity areas. For example, salinity changes during a tidal cycle in the upper estuary can be as high as 5 ppt within 12 hours, whereas less than 3 ppt change is common in the down-estuary areas (Boesch 1971). Long-term monitoring throughout Chesapeake Bay also shows that the variance in salinity (standard error of the mean) increases with decreasing salinity in the James, York, and Rappahannock Rivers (Dauer et al. 1989). In addition, temperature at the mouth of the river is more stable than in the rest of the river because of the relative proximity to oceanic influence (Boesch 1971). Physical disturbance from sediment deposition is also greater upriver, usually near the turbidity maximum (L. Schaffner, personal communication).

Changes in physical characteristics are likely to have profound effects on the activities of resident fauna, such that lower salinity areas are more stressful (Menge and Olson 1990). This may be especially true in estuaries where many species are of marine origin (Remane and Schlieper 1971). Changing salinity requires osmoregulation which is costly in terms of energy expenditure, and low salinity may be additionally harsh for species with marine origins. Infauna are immobile and are evolutionarily adapted to their surrounding environmental fluctuations. Conversely, predators are able to migrate,

therefore they can escape undesirable environmental conditions and need not be physiologically adapted to a harsh physiological environment. For instance, though the blue crab has a wide salinity tolerance (Mangum and Towle 1977), growth and feeding efficiency are higher at higher salinities (Cadman and Weinstein 1988). Though the blue crab is characterized as euryhaline, below suboptimal salinities (~27ppt), respiration rate increases (Colvocoresses et al. 1974, Mangum and Towle 1977) and varies inversely with salinity due to higher energy demands of osmotic regulation at low salinity (Findley et al. 1978). For instance, in the non-tidal Baltic where there are steep gradients in salinity, few epibenthic predators occur due to the salinity stress (Bonsdorff and Blomqvist 1993). Temperature stress may also affect predators migrating into and out of upriver areas. For instance, ventilation rates in some estuarine fish (e.g., *Trinectes maculatus*, *Morone americana*, and *Leiostomus xanthurus*) significantly increased after temperature increases of 2.5 to 5°C (Burton 1979). Hence, predators are likely to be more stressed upriver.

***Measures of diversity***

Diversity measures are central to understanding community ecology (MacArthur 1965, Whittaker 1972, Peet 1974, Pielou 1975, Grassle et al. 1979, Lande 1996). According to Lande (1996), "a good measure of diversity should ideally be *nonparametric* and *statistically accurate.*" Though there are many diversity indices, each of which seeks to characterize the diversity of a sample or community with a single statistic (Magurran 1988), the most frequently used measures are nonparametric and do not depend on a particular species abundance distribution from which the natural community will likely

deviate (e.g., log series, Fisher et al. 1943; broken stick, MacArthur 1957; or lognormal, Preston et al. 1948).

Two key parameters characterize diversity, richness (i.e., the number of species) and evenness (i.e., equitability across all species). Other measures include indices such as the Shannon-Wiener information index H' and Simpson's diversity ($1-\lambda$), which are based on species frequencies (Magurran 1988). Diversity has also been described as within and among communities (alpha and beta diversity, respectively) and total diversity in a set of communities (gamma diversity; Whittaker 1972, Ricklefs and Schulter 1993). Lande (1996) defines the different measures and I summarize them here.

- *Species richness* is simply the number of species in a community. This is the most basic measure of diversity because the data is relatively easy to collect, however, it can be biased because rare species are often absent from samples.
- *Evenness* is the division of individuals among the species and is also a commonly used measure.
- *Shannon-Wiener Diversity, H'* (Shannon and Wiener 1962), is the average information per individual described by

$$H' = \sum_{i=1}^{S} p_i \ln p_i \qquad (1)$$

For a given number of species, the information reaches its maximum value when all species (S) are equally frequent in the community, and $p_i$ is the number individuals of species $i$. In practice, this index increases with the number of species in a

community and will not go above five. This is a popular measure of diversity and thus is comparable across many studies; however, it may be biased depending on the number of species in a community (Hutcheson 1970). In speciose communities, this measure of diversity may be inaccurately low if few individuals are sampled. Accurate estimation of H' requires sampling large numbers of individuals (more than twice the number of species in the community; Lande 1996).

- *Simpson's concentration*, $\lambda$ (Simpson 1949), is the probability that two randomly chosen individuals from a given community are the same species. It is described by

$$\lambda = \sum_{i=1}^{S} p_i^2 \qquad (2)$$

where $p_i$ is the number of individuals of species $i$.

- *Simpson's diversity* = $1 - \lambda$

is the probability that two randomly chosen individuals are different species. This can be an unbiased estimator that accurately extrapolates species diversity, even from a small sample size. Though many indices are used, a recent statistical evaluation of diversity indices determined that the most accurate estimation of total species diversity based on random sampling uses an ANOVA for Simpson's diversity (Lande 1996).

*Benthic communities and their predators*

The benthos in Chesapeake Bay comprises diverse assemblages of species (Diaz and Schaffner 1990). Shallow-water assemblages in unvegetated areas of Chesapeake Bay are less dense and diverse than comparable vegetated areas (Orth 1977). Vegetation may provide partial refuge from predation for infauna, as it is difficult for predators to forage and dig through the rhizome mats of seagrass. In addition, infaunal densities are lowest in summer and fall, during and after the period when predators are abundant in the system (Hines et al. 1987, 1990). Thus, predation appears to be a primary biotic factor influencing species abundances, at least in high salinities (Virnstein 1977, 1979) and likely governs infaunal community structure.

The numerous predation experiments in soft sediments present contradictory findings regarding epibenthic predator effects on infaunal prey abundance and diversity. In some cases, abundance and species richness have increased with predator exclusion (Commito 1976, Virnstein 1977, 1979, Reise 1977, 1978, 1985, Bell and Coull 1978, Peterson 1979, Woodin 1981, Botton 1984); whereas in other instances, the effects of predation are minimal (Berge and Hathagen 1981, Thorp and Bergey 1981, Choat and Kingett 1982, Ward and Fitzgerald 1983, Raffaelli and Milne 1987, Jaquet and Raffaelli 1989, Mattila et al. 1990, Bonsdorff et al. 1986, Mattila and Bonsdorff 1989). Some inconsistencies have been explained by the presence of small or infaunal predators that are not excluded by exclusion cages (Ambrose 1982, 1984, Virnstein 1978). Though much has been gained from earlier investigations, conclusions from one location may not be

broadly applicable and further experimentation with predation in soft sediments is warranted.

In Chesapeake Bay, the main epibenthic predators include the blue crab (*Callinectes sapidus*), two sciaenids, spot (*Leiostomus xanthurus*) and Atlantic croaker (*Micropogonias undulatus*), and two flatfish, the hogchoker (*Trinectes maculatus*) and the summer flounder (*Paralichthys dentatus*) (Virnstein 1977, Mansour 1992). Despite intense predation , there does not appear to be a keystone predator (sensu Paine 1966) in this system (Hines et al. 1990).

These bottom-feeding predators either migrate into or become active in Chesapeake Bay and its tributaries in the spring, feed throughout the summer and early fall, and then cease to feed or emigrate in the fall (Hines et al. 1987, McErlean et al. 1973). Many of these predators feed on infauna, consequently affecting benthic abundance and diversity (Virnstein 1979); predation effects of epibenthic crustaceans, such as the blue crab, can be greater than the effects of epibenthic fishes (Nelson 1981, Botton 1984, Quammen 1984, Gee 1987). A focus on predation intensity must incorporate not only the identification of predatory species, but also the abundance and effectiveness of those predators (Menge 1983).

In addition to the common epibenthic predators, infaunal predators can also influence abundances of other infauna (Roe 1976, Riese 1979, Ambrose 1982, 1984, Commito 1982, Oliver et al. 1982). Many infaunal predators, such as nemertean worms, increase in abundance with predator exclusion, and subsequently decrease abundance of their infaunal prey (e.g., small polychaetes such as *Paraprionospio pinnata*,

*Scolecolepides viridis* and *Peloscolex gabreillae*; Holland et al. 1980). This suggests that the prey of predatory infauna may be less abundant in the absence than in the presence of epibenthic predators (Ambrose 1984). Therefore, results of caging studies must be interpreted with caution.

The system of interest in this study is the York and Rappahannock River tributaries of Chesapeake Bay. The estuarine gradient is mainly a salinity gradient, but other environmental factors vary concurrently (see Boesch 1977, Dauer et al. 1989). Many environmental variables increase in variance upriver in this system (i.e., salinity, turbidity, and temperature - to a lesser degree). For example, comprehensive monitoring throughout the York, James and Rappahannock Rivers showed increased variance in salinity with distance upriver (Dauer et al. 1989). Some variables, however, such as oxygen stress in channels (Phil et al. 1992) and bottom disturbance are negatively correlated with salinity.

### *Caging effects*

Most experiments dealing with the effect of predation on the benthos employ predator exclusion cages, which have been utilized in rocky intertidal habitats to elucidate the importance of competition and predation in community regulation (Connell 1972, 1975); similar effects have been detected in some soft-bottom systems (Virnstein 1977, 1979, Peterson 1979b, Holland et al. 1980, Dayton 1984, Quammen 1984, Hines et al. 1990). Other investigations have shown weak responses of prey to predator removal, although these cases may be underreported (Hall et al. 1990). Additionally, weak

responses may be detected at one time of year, when strong responses may occur at another (Summerson and Peterson 1984). Some difficulties arise in the use of cages due to caging artifacts (see Virnstein 1978), such as reduced current flow and or increased deposition of sediments (McCall 1977). Such sedimentation can be either beneficial or detrimental, by suffocating suspension-feeders or increasing food for deposit-feeders, respectively (Peterson 1979b, Hulberg and Oliver 1980). If caging experiments are carefully planned and interpreted, they can be useful in determining the role of predation in benthic systems.

*Goals and hypotheses*

This study was designed to answer the question "does the effect of predation upon benthic community structure change along an estuarine gradient in the York River?" and "do the current models of benthic community regulation apply to soft-bottom systems?" Specifically, I attempted to do four things, to determine (1) natural **benthic species diversity** (richness, H' and Simpson's diversity, 1 - $\lambda$) in shallow water at two different zones (upriver and downriver) along the York River, (2) **caging artifacts & effects** on predator behavior (examined in the laboratory), sediment grain size, and nutrient deposition (e.g., carbon and nitrogen levels), (3) natural **predator abundance** in two zones in two rivers throughout the summer predation period, and (4) the **effect of predation** on benthic community structure by using predator removal or enhancement and consequent changes in species richness, evenness, or diversity (H' and Simpson's diversity, 1-$\lambda$) within the two zones. In this paper "community" will refer to an assemblage of

macrobenthic populations at specific sites, and the patterns of community structure will be described using various indices that will be quantitatively compared using statistical methods.

My hypotheses were that (1) as in deep water areas, species diversity in shallow water habitats would decrease further upriver, away from ocean access, (2a) predators would have no access to the benthos within 'full cages', intermediate access to open sediment, and enhanced activity around and inside of partial cages, and (2b) cages would not significantly increase deposition of fine sediments and nutrients (3) predators would be more abundant upriver (based on deep-water abundances), and, based on Menge and Sutherland's consumer stress model, (4) the effect of predation would be greater in downriver, lower stress areas and thus community structure would show greater change with predator exclusion or enhancement downriver.

## *METHODS AND MATERIALS*

### Study area

All studies in this dissertation were conducted in shallow subtidal habitats of the York and Rappahannock Rivers, tributaries of Chesapeake Bay. These areas were selected at 1-2 m depths, were unvegetated and had muddy-sand sediments. Study sites were set up in the York and Rappahannock Rivers, at two salinity zones per river, the upper mesohaline zone at about 15-20 ppt (referred to as downriver) and the lower mesohaline zone at about 5-10 ppt (referred to as upriver). Four York upriver sites were approximately 25 miles from the mouth of the River and located near West Point, whereas the four downriver sites were approximately 5 miles from the mouth, near Gloucester Point (Fig. 2.2, Table 2.1a). On the Rappahannock River, the four upriver sites were approximately 30 miles from the mouth, near Bowler's Rock, and the four downriver sites were approximately 10 miles from the mouth, near Urbanna. The four sites in each salinity zone were established using a grid of random locations at shallow depth and in muddy-sand sediments. Two sites were located at each of the northern and southern shores of the Rivers in both salinity zones. Field experiments on macrobenthic community structure were conducted throughout the summers of 1992 and 1993, whereas trawling for predator abundance was conducted in the summer of 1994. Analysis of benthic data was conducted using an analysis of variance (ANOVA; Table 2.1b). In summary, the experimental design was as follows.

Fig. 2.2. Sampling zones (filled circles) on the York River. Four sites at the upriver zone near West Point, and four sites downriver near Gloucester Point.

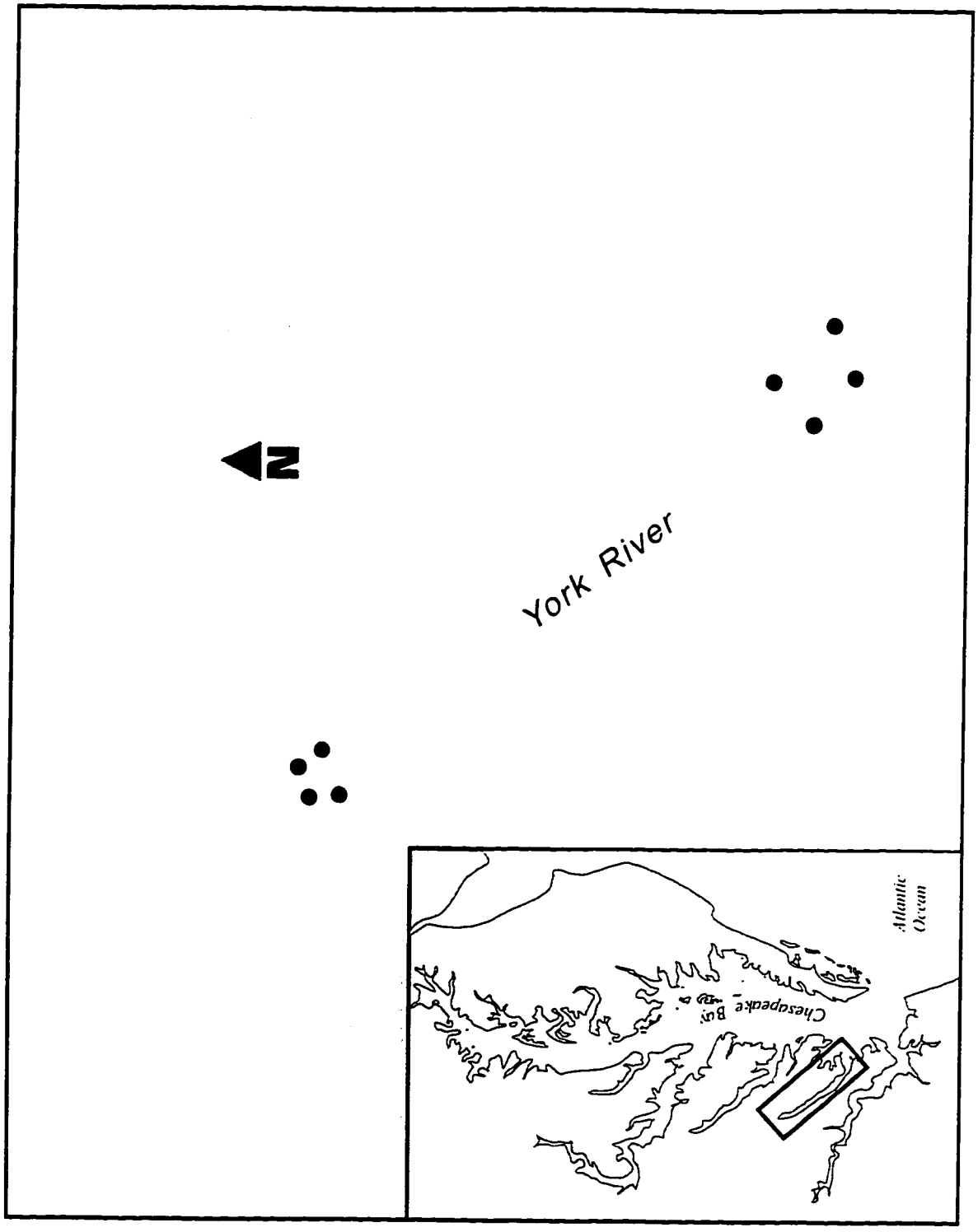


Table 2.1a. Summary of experimental sampling sites where predator exclusion cages were established and environmental parameters. Y = York River, H = high salinity, downriver. Salinities and Temperatures are means of values measured at sampling sites (n = 6). SE = Standard Error. Sediment samples taken in each cage at initial deployment of the cages. Depth is the maximum observed at high tide.

| SITE - SHORE | LATITUDE LONGITUDE | SALINITY (ppt)/ TEMP (°C) (mean ± SE) | SEDIMENT % Gravel, % Sand | SEDIMENT % Silt & Clay | DEPTH (meters) |
|---|---|---|---|---|---|
| YH1-NE | 37°15.092 N<br>76°30.451 W | 19.0 ± 0.52<br>23.0 ± 2.42 | 0.06,<br>86.52 | 13.41 | 2.0 |
| YH2 - NW | 37°18.122 N<br>76°33.648 W | 18.2 ± 0.75<br>23.5 ± 2.44 | 0,<br>81.77 | 18.23 | 1.5 |
| YH3 - SE | 37°15.727 N<br>76°32.801 W | 19.2 ± 1.01<br>23.8 ± 2.39 | 0,<br>83.12 | 16.88 | 1.5 |
| YH4 - SW | 37°16.194 N<br>76°33.462 W | 18.3 ± 0.80<br>23.3 ± 2.25 | 0.05,<br>84.64 | 15.31 | 2.0 |
| YL1 - NE | 37°27.589 N<br>76°43.432 W | 11.8 ± 0.58<br>24.2 ± 2.33 | 0.45,<br>62.95 | 36.60 | 1.5 |
| YL2 - NW | 37°27.790 N<br>76°43.542 W | 11.6 ± 0.60<br>12.2 ± 0.58 | 0.23,<br>78.00 | 21.77 | 1.5 |
| YL3 - SE | 37°15.092 N<br>76°30.451 W | 11.6 ± 0.60<br>24.3 ± 2.34 | 0,<br>84.40 | 15.60 | 2.0 |
| YL4 - SW | 37°26.818 N<br>76°44.884 W | 12.2 ± 0.58<br>24.6 ± 2.46 | 0.53,<br>61.96 | 37.51 | 1.0 |

Table 2.1b. Potential Analysis of Variance Model displaying all factors used in this study. In practice only some of these factors were used in any one ANOVA (e.g., Cage type x Zone for York River only).

$$x_{ijklm} = \mu + C_i + L_j + R_k + D_l + Z_m + S_m + C_iZ_j + C_iR_k + C_iD_l + Z_jR_k + Z_jD_l + R_kD_l + C_iR_kD_l + C_iZ_jR_k + C_iZ_jD_l + Z_jR_kD_l + Z_jR_kC_iD_l + e_{ijklm}$$

| FACTORS | VARIABLE | FACTOR TYPE | LEVELS | DESCRIPTION |
|---|---|---|---|---|
| Cage Type | $C_i$ | Crossed | 5 | Five cages |
| Zone | $Z_j$ | Crossed | 2 | Upriver, Downriver |
| River | $R_k$ | Crossed | 2 | York, Rappahannock |
| Date | $D_l$ | Crossed | 3 | July, Aug., Oct. |
| Site | $S_m$ | Blocked | 4 | NE, NW, SE, SW |

- 2 Rivers: York, Rappahannock;
- 2 zones per River: 'Downriver' = Upper-Mesohaline (18-20 ppt), and 'Upriver' = Lower-Mesohaline (7-10 ppt);
- 4 Replicate sites per zone: 2 on the south side, 2 on the north side of the river;
- 5 caging treatments per site: 'full cage', 'roof only', 'sides only', 'cage control' and 'no cage'.

## I. BENTHIC SPECIES DIVERSITY

Cages were deployed in July to reduce caging influence on infaunal recruitment; the maximum reproduction and recruitment of infaunal organisms in Chesapeake Bay are between February and May (Mountford et al. 1977). Because predators are active in the system in warm summer months, this study was conducted throughout the mid-summer, and early fall 1992-1994.

At each study site, a grid was set up whereby plots were separated by 3 m. One of the five predator-exclusion cage treatments was randomly assigned to each plot. The full experiment consisted of 80 cages (2 rivers x 2 salinity zones x 2 shores per river x 2 sites per shore x 5 cage treatments). I used five different cage designs of 1-$m^2$ PVC-framed, mesh-covered square cages. Two cage types excluded specific predators ('full cage', 'sides only'), two of the five types ('roof only', 'cage control') attracted predators, thus enhancing

predation, and one cage type ('no cage') allowed natural predators complete access to cages. Each cage type and its purpose is described below:

*'full cage'*- A 1-$m^2$ frame extended 25 cm above the sediment surface, and was covered on all sides with 1.5-cm mesh. A 20-cm deep aluminum skirt extended from the bottom of each cage into the sediment to prevent migration of infauna or digging by predators. This cage was designed to exclude all predators greater than 1.5 cm from access to the benthos. All evidence suggests this cage design was effective (except occasionally I found a crab inside this treatment, but it was immediately removed and the cage repaired).

*'roof only'*- This cage only extended 5 cm off the sediment surface, had no mesh on the sides and only mesh on the roof. It was designed to exclude many of the epibenthic fishes, but allow access by crabs through 5-cm-high openings on the sides. Because it provided structure, this cage type actually enhanced predator activity (see cage artifacts & effects results).

*'sides only'*- This cage had four sides of mesh and no roof. It was designed to exclude predators approaching from the sides (e.g., flatfish or rays), and turned out to be effective at excluding most predators (see cage artifacts & effects results).

*'cage control'*- This cage had a similar frame as the 'full cage', but was only covered on 2 sides and half the roof with mesh. It was designed to allow access by all predators and to affect the hydrodynamics similar to the 'full cage'. Because of the structure provided, this cage enhanced predator activity (see cage artifacts & effects results).

*'no cage'*- This cage consisted of a 1-$m^2$ flat frame placed on the sediment surface, marking an area of sediment to be sampled. It allowed access by all predators at their natural abundance (see cage artifacts & effects results).

*Procedures:* Initially, macrobenthic infauna were sampled when cages were deployed. Three subsamples were taken at random grid coordinates within each cage with a 8.8-cm diameter PVC core (0.006 $m^2$) to a depth of 20 cm. Samples were brought to the surface and sieved through a 500-$\mu$m screen. Samples were stored in cloth bags and submerged in 10% buffered Formalin with Rose bengal stain at the laboratory. Infauna were sampled 6 weeks and 12 weeks after cage deployment.

Every sampling period, a 3-cm diameter core was taken in the center of each cage for surface-sediment grain-size analysis following the methods of Folk (1968). Salinity and water temperature were also recorded. Cages were checked for integrity and fouling organisms every 1-2 weeks, and repaired or scrubbed as necessary.

Macrofauna were removed from sediments and detritus using a two-step process. First, elutriation separated lighter organic material and most organisms from heavier sediment. The elutriate was sorted with a dissecting microscope. The heavy sediment fraction was sorted without a microscope, after spreading the material in a pan with some water. The samples were initially sorted into phylogenetic groups, and later identified to the lowest possible taxonomic level. The abundance of all species were recorded. Rarefaction curves were used to determine the number of subsamples needed for a standardized species count (Krebs 1989). For rank abundance in the natural community, the total number of individuals collected from all 3 subsamples at all four sites within a

zone were compiled and compared. Diversity indices such as richness (S), evenness (J), Shannon-Wiener diversity (H'), and Simpson's diversity ($1-\lambda$) as well as abundance were determined for each sample using a computer program developed by Youngseuk Park. For each treatment replicate, the three subsamples were averaged and Analysis of Variance models run (Minitab 1993) to determine differences in diversity among cage treatments, river (salinity) zones, replicate sites, and sampling dates. In conducting this caging experiment, a critical assumption was made; it was assumed that the infauna within the areas where cages were deployed were homogeneously distributed, so that each cage initially enclosed the same infaunal community.

## II. CAGING ARTIFACTS & EFFECTS

### A. Laboratory predator behavior

Efficiency of predator exclusion cages was evaluated in a laboratory experiment using large experimental mesocosms and video cameras to quantify predator behavior around cages. Poor water clarity in the York and Rappahannock Rivers limited the ability to quantify the behavior of predators around predator exclusion cages in the field. These laboratory experiments were conducted in a computer-controlled laboratory setting, the Glucksman Experimental Mesocosm (GEM) facility.

*Procedures:* Fish and crabs were collected using a 4.9-m otter trawl towed near the field cages (See "predator abundance" procedures below). Animals were maintained in 1m x

2m x 1m holding tanks until needed and were starved for at least 24 hours prior to experimentation.

Two 3,500 liter, 2m x 3m x 2m mesocosm tanks were filled with approximately 20 cm of sand, and seawater was added to a level 40 cm above the sand. One of five cage treatments ('full cage', 'sides only', 'roof only', 'cage control' or 'no cage') was placed in the center of each mesocosm and buried to a level similar to that of field cages.

For each trial the experimental cage was baited in the center with a chopped bloodworm. A predator was randomly selected from the following group: blue crab (*Callinectes sapidus*), Atlantic croaker (*Micropogonias undulatus*), spot (*Leiostomus xanthurus*), and flatfish (either hogchoker, *Trinectes maculatus*, or summer flounder, *Paralichthys dentatus*). The predator was measured, placed into a large mesh basket within the mesocosm, and allowed to acclimate for five min. Predators from a range of sizes were used: blue crabs 50-149 mm CL, spot 95-195 mm TL, croaker 95-223 mm TL, flatfish 70-141 mm TL. An IR-sensitive camera above each mesocosm was positioned so that the cage and approximately 20 cm around the perimeter were visible. A red light automatically switched on with all other room lights off.

The predator was released from the mesh acclimation basket and allowed to roam the tank. Video recording was maintained for two hours after the predator was released. Activity was registered if the animal was inside the cage and this total time spent was compared between predators and treatments. At the conclusion of a trial, the predator and bait were removed and the same procedure was repeated for the next randomly selected predator and cage. Two replicate trials for each predator for each cage type were

conducted. The total time over the two hour period that each predator was "in" each cage was computed and averaged for the two replicates of each treatment. Any significant differences between activity of species within different cage types was determined using ANOVA.

**B. Sediment and nutrient analysis**

Cage effects or artifacts were determined by several means including an examination of the efficiency of predator exclusion (see **Laboratory predator behavior** above), analysis of sediment grain size alterations, and an indirect analysis of flow using Carbon Hydrogen Nitrogen (CHN) measurements. Differences in sediment composition from one time period to another within a cage would be due to cage effects on current flow and sediment availability at the time. Difference between a particular cage treatment and the natural sediment (e.g., 'no cage') would indicate an effect of that cage on sediment deposition.

*Procedures:* Cages were visually examined each sampling period to determine if they were excluding the desired predators, though low visibility may have reduced detectability. Sediment samples for grain size analysis were taken with a 3-cm diameter core to 5 cm depth in each cage at each sampling period to quantify flow-mediated changes in sediment type. Sediment particle size distribution was determined by sieve and pipette analysis (Folk 1968). In addition, to test for modifications of food deposition rates to the sediment surface, one randomly selected cage of each type at each salinity per river was selected for CHN analysis (20 samples total). Each CHN sediment sample was taken from the top 0.5-

1 cm of sediment, where labile organic deposition should be highest, and was frozen until analysis. Total organic carbon was determined by high temperature combustion and analysis of gas chromatograms by VIMS analysis personnel (Menzel and Vaccaro 1964)

## III. PREDATOR ABUNDANCE

To determine any differences in predator species composition, abundance or size, trawling was conducted within the two zones (upriver and downriver) used for benthic caging experiments. Trawling is a proven method of evaluating predator abundance in marine and estuarine systems (Hines et al. 1987), including tributaries of Chesapeake Bay such as the York and Rappahannock Rivers (Lipcius and Van Engel 1990).

*Procedures:* At each of the four replicate upriver and downriver sites per river, abundance of predators in the vicinity of the cages was quantified using a trawl in 1-2 meters of water. Demersal fishes and crabs were collected with a 4.9-m semi-balloon otter trawl (3-m wide mouth, 5-cm-mesh net body, and 7-mm-mesh cod end). Two 2-min tows were taken parallel to shore at each site, one with the tidal current, and one against the tidal current. Distance traveled during each tow was estimated using a GPS unit. Both trawls were compiled and analyzed as one sample. Thus, four replicate samples were taken in each of the upriver and downriver zones. Animals in each trawl were identified, counted and measured (fish: total length, crabs: carapace width). Sampling was repeated monthly May through August, 1994. Variation in epibenthic predator abundance was analyzed as a function of river, zone (upriver vs. downriver) and month using a full-factorial, fixed-effects analysis of variance model (Underwood 1981).

# *RESULTS*

## I. BENTHIC SPECIES DIVERSITY

### A. A description of the natural community

Downriver, over 32 species were collected over four sites; ten of the species were abundant, accounting for 63% of the individuals collected. Dominant infaunal species in the natural community at the initiation of sampling (week 0- July 1992) were compared by determining rank dominance (Table 2.2). Dominants included many deposit-feeding polychaetes, including the head-down feeding *Heteromastus filiformis* and *Clymenella torquata*, and the surface-feeding *Tharyx* sp., *Streblospio benedicti*, and *Spiophanes bombyx*, along with the predatory *Nereis succinea* and *Glycinde solitaria*. Among other taxa were a suspension-feeding phoronid, *Phoronis psammophila*, the amphipod, *Listriella clymenellae*, often associated with *C. torquata* tubes, and a small gastropod *Acteocina canaliculata*. There were, however, no common bivalves downriver. The study sites and associated infauna were typical of shallow, unvegetated muddy-sand shoals in the mid to upper York River. Seventy taxa across both zones were accumulated (Appendix I).

Upriver, dominants comprised polychaetes, including the head-down deposit-feeding *Heteromastus filiformis*, the surface deposit feeding *Streblospio benedicti*, and the predatory *Nereis succinea*. Among other taxa, *Macoma balthica*, a facultative surface- or deposit-feeding bivalve was common, as well as deposit-feeding tubificids. A total of 13

Table 2.2. Dominant infaunal species rank and total abundance in the natural community at the initiation of the benthic diversity experiment in July 1992 (week 0). Dominance determined by species having more than 85 individuals/$m^2$. Abundance was determined as the sum of individuals collected in three cores from all 4 replicate sites (total area = 0.07 $m^2$) at each river zone. P= polychaete, B = bivalve, O = oligochaete, A = amphipod, Ph = phoronid, G = gastropod. * = common to both river zones.

| Species | Rank | #Indiv./ $m^2$ |
|---|---|---|
| **UPRIVER:** | | |
| *Heteromastus filiformis* (P) * | 1 | 412 |
| *Macoma balthica* (B) | 2 | 355 |
| *Streblospio benedicti* (P) | 3 | 270 |
| *Nereis succinea* (P) | 4 | 270 |
| Tubificidae (O) | 5 | 114 |
| **DOWNRIVER:** | | |
| *Heteromastus filiformis* (P) * | 1 | 540 |
| *Tharyx* sp. (P) | 2 | 398 |
| *Clymenella torquata* (P) | 3 | 341 |
| *Streblospio benedicti* (P) | 4 | 284 |
| *Listriella clymenellae* (A) | 5 | 241 |
| *Nereis succinea* (P) | 6 | 170 |
| *Acteocina canaliculata* (G) | 7 | 142 |
| *Phoronis psammophila* (Ph) | 8 | 128 |
| *Spiophanes bombyx* (P) | 9 | 114 |
| *Glycinde solitaria* (P) | 10 | 85 |

species was collected over four sites (Table 2.2). Most species were polychaetes, with some bivalves, amphipods and gastropods. Of those, five were relatively abundant (having greater than five individuals over the four sites), and accounted for 83% of the individuals sampled.

During week 6, species' rank dominance depended on cage treatment (Table 2.3). Downriver, 6 polychaete, 1 mollusc, 1 amphipod and 1 phoronid species were abundant. Upriver, 4 polychaete species, 2 mollusc species and oligochaetes were abundant.

**B. Diversity in the natural community**

Diversity in this study was compared using two main indices, Shannon-Wiener diversity (H') and Simpson's diversity (1-$\lambda$). The Shannon-Wiener index is commonly used and thus, results here can be easily compared with other studies; however, this index is greatly influenced by number of individuals collected and therefore may be unreliable at low abundance. Simpson's diversity is not affected by sample size and therefore gives a reliable estimate of species diversity.

Diversity of the benthic natural communities was significantly higher downriver than upriver (Table 2.4). Across all time periods, mean H' diversity downriver was 2.89 $\pm$ 0.02 SE, compared to 2.08 $\pm$ 0.02 SE upriver. Mean 1-$\lambda$ was 0.81 $\pm$ 0.07 SE downriver, compared to 0.74 $\pm$ 0.07 SE upriver. The natural community was followed through time in the 'no cage' treatments and differences in river zone (downriver and upriver), and time (week 0, 6 and 12) were compared. Variance in H' diversity between zones was homogeneous (Bartlett's test, $P = 0.927$), therefore raw data were used for the ANOVA.

Table 2.3. Dominant infaunal species rank for each treatment at 6-weeks sampling. Dominance determined by species having more than 85 individuals/$m^2$. FC = 'full cage', RO = 'roof only', SO = 'sides only', CC = 'cage control' and NC = 'no cage'. P = polychaete, B = bivalve, O = oligochaete, A = amphipod, Ph = phoronid, G = gastropod. * = common to both river zones. The symbol - means not ranked in top ten for that cage treatment.

| Species | Rank | | | | |
|---|---|---|---|---|---|
| | FC | RO | SO | CC | NC |
| **UPRIVER:** | | | | | |
| Tubificidae (O) | 1 | 2 | 1 | 1 | 4 |
| *Nereis succinea* (P) * | 2 | 1 | 4 | 3 | 3 |
| *Heteromastus filiformis* (P) | 3 | 4 | 3 | 2 | 1 |
| *Streblospio benedicti* (P) | 5 | 5 | 2 | 5 | 2 |
| *Macoma mitchelli* | 4 | 3 | 5 | 4 | 5 |
| *Macoma balthica* (B) | 7 | 6 | 7 | 6 | 6 |
| *Glycinde Solitaria* (P) | 6 | 7 | 6 | 7 | 7 |
| **DOWNRIVER:** | | | | | |
| *Mercenaria mercenaria* (M) | 1 | 1 | 2 | 5 | 1 |
| *Mediomastus ambiseta* (P) | 2 | 3 | 1 | 1 | 7 |
| *Nereis succinea* (P) * | 3 | 5 | 5 | 3 | 6 |
| *Glycinde solitaria* (P) | 4 | 6 | 3 | 2 | 2 |
| *Clymenella torquata* (P) | 6 | 4 | 4 | 10 | 3 |
| *Spiophanes bombyx* (P) | - | 8 | 8 | 10 | 8 |
| *Phoronis psammophila* (Ph) | 7 | 2 | 7 | 4 | 4 |
| Amphipoda (A) | 10 | 9 | 6 | 8 | 5 |
| *Tharyx* sp. (P) | 5 | - | 10 | - | - |

Table 2.4. Benthic diversity through time for the natural community ('no cage' treatment). ANOVA factors include Zone (downriver and upriver), Time (week 0, 6 and 12), blocked by Site (four replicate sites in each zone). Variance in H' diversity was homogeneous, therefore raw data were used for the ANOVA. Variance in λ was heterogeneous, thus data was log-transformed for use in the ANOVA.

| Measure | Source of variation | SS | df | MS | F |
|---|---|---|---|---|---|
| Shannon-Wiener (H') | Zone | 3.95 | 1 | 3.95 | 37.74**** |
| | Time | 0.28 | 2 | 0.14 | $1.34^{ns}$ |
| | Zone x Time | 0.14 | 2 | 0.07 | $0.70^{ns}$ |
| | Site | 0.17 | 3 | 0.06 | $0.54^{ns}$ |
| | Error | 1.57 | 15 | 0.10 | |
| | Total | 6.12 | 23 | | |
| Simpson's index (log λ) | Zone | 0.11 | 1 | 0.11 | 9.82** |
| | Time | 0.03 | 2 | 0.01 | $1.16^{ns}$ |
| | Zone x Time | 0.21 | 2 | 0.10 | 9.06*** |
| | Site | 0.01 | 3 | 0.00 | $0.22^{ns}$ |
| | Error | 0.17 | 15 | 0.01 | |
| | Total | 0.52 | 23 | | |

**** $P < 0.001$, *** $P < 0.005$, ** $P < 0.01$, $^{ns}$ $P > 0.05$.

Variance in $\lambda$ was heterogeneous between zones (Bartlett's test, $P = 0.001$ ), thus data was log-transformed and this data with homogeneous variance (Bartlett's test, $P = 0.32$) was used in the ANOVA. Throughout the sampling period, there was higher diversity downriver (as determined by both H' and $1-\lambda$; Table 2.4). There was a significant Zone x Time interaction for $1-\lambda$, thus, zones were compared separately for each time period. At week 0, there was no significant difference between Simpson's diversity downriver and upriver (ANOVA, df = 7, MS = 0.02, F = 2.00, $P = 0.21$). At week 6, diversity was significantly higher downriver (ANOVA, df = 7, MS = 0.09, F = 9.46, $P = 0.02$), and at week 12 diversity was significantly higher downriver (ANOVA, df = 7, MS = 0.20, F = 36.94, $P = 0.001$). Overall, in the natural benthic community, diversity was greater downriver, and did not change significantly throughout the summer and fall. This is in agreement with Menge and Sutherland's 1987 model that predicts higher salinity in less stressful, more stable environments.

The diversity of infaunal predators was similar upriver and downriver (only two species each zone) but the total abundance was slightly greater upriver (293 individuals upriver, 232 individuals downriver). At the 12-week sampling, the mean density of *Nereis succinea* downriver was $1278 \pm 511$, whereas the density upriver was $4573 \pm 833$ individuals/$m^2$. For the predatory *Glycinde solitaria*, density was greater downriver at $1945 \pm 548$, than upriver at $833 \pm 45$ individuals/$m^2$. Though nemerteans are typically found in high salinity, few were captured by my sampling method. Thus, any differences in predation were not likely due to difference in infaunal predators.

For the natural community, there was significant variation between sites for some diversity measures. Upriver, H' was significantly different between sites (ANOVA df = 11, F = 4.83, $P = 0.033$), as was $\lambda$ (ANOVA df = 11, F = 9.34, $P = 0.005$). Downriver, a significant difference between sites was only found for abundance (ANOVA df = 11, F = 14.62, $P = 0.001$). High variability in benthic infauna between sites may indicate that physical characteristics vary substantially between sites, and may further suggest that conclusions from a single site are not applicable throughout the river. Because of the high variation between sites, all subsequent analyses were blocked by site.

## C. Caging Experiments

### *1. Abundance differences for two rivers - Week 6*

At week 6, abundance was analyzed for two rivers, the York and Rappahannock. In the York, abundance was not significantly different downriver compared to upriver, nor were there treatment effects, but there was a significant difference due to site (Figure 2.3a, b, Table 2.5). In the Rappahannock River, abundance was significantly higher downriver, but there was no significant caging effect or site effect (Figure 2.3c, d, Table 2.5). In both rivers, there was high variability between sites, and few treatment effects that could be detected after 6 weeks. Due to time limitations and labor involved in the sorting and identification of all benthic samples, Rappahannock benthic samples were not identified to species and no diversity comparisons were made for this river. It appeared that there were similar, if not stronger, effects of predator exclusion on the benthos of the Rappahannock as there were on the York (Fig. 2.3).

Fig. 2.3. Abundance of benthic invertebrates at 6-weeks sampling (September 1993) for five different caging treatments. Mean + Standard Error from 4 replicate sites at each river and zone combination: (a) York Downriver, (b) York Upriver, (c) Rappahannock Downriver, (d) Rappahannock Upriver. Notice high standard deviations associated with the means because of substantial variation within each site.

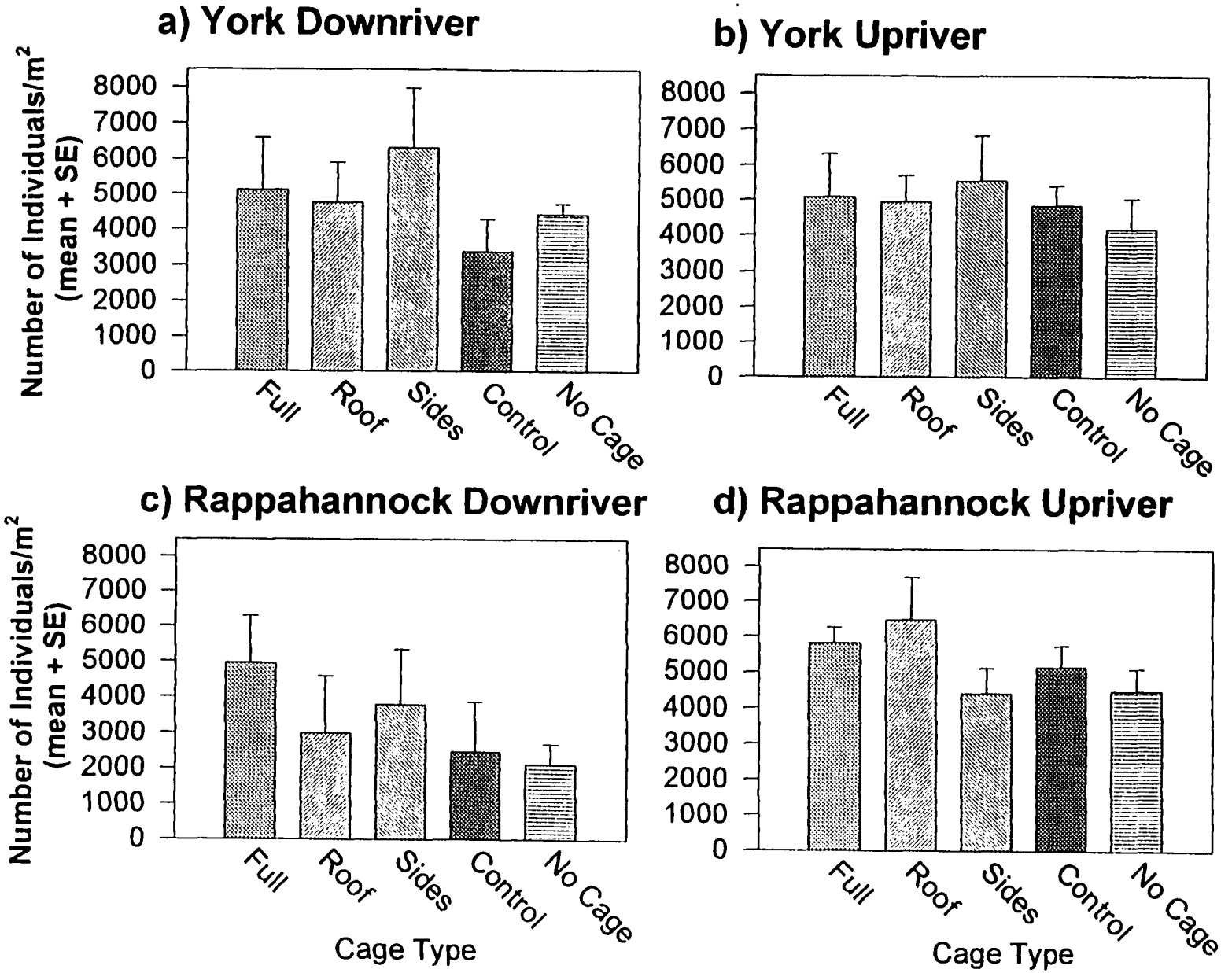


Table 2.5. Benthic abundance of infauna at the **6-Week** sampling for both the Rappahannock and York Rivers. ANOVA factors consisted of Cage type ('full cage', 'roof only', 'sides only', 'cage control' and 'no cage'), Zone (Downriver and Upriver), blocked by Site (four replicate sites in each zone).

| Measure/ River | Source of variation | SS | df | MS | F |
|---|---|---|---|---|---|
| Abundance/ Rappahannock | Cage Type | 825.2 | 4 | 206.3 | $1.42^{ns}$ |
| | Zone | 1435.5 | 1 | 1435.5 | 9.99*** |
| | Cage x Zone | 364.4 | 4 | 91.1 | $0.36^{ns}$ |
| | Site | 980.3 | 3 | 326.8 | $2.25^{ns}$ |
| | Error | 3928.9 | 27 | 145.5 | |
| | Total | 7552.3 | 39 | | |
| Abundance/ York | Cage Type | 598.4 | 4 | 149.6 | $1.22^{ns}$ |
| | Zone | 5.0 | 1 | 5.0 | $0.04^{ns}$ |
| | Cage x Zone | 199.3 | 4 | 49.8 | $0.41^{ns}$ |
| | Site | 1785.5 | 3 | 595.2 | 4.84** |
| | Error | 3318.6 | 27 | 122.9 | |
| | Total | 5906.8 | 39 | | |

*** $P < 0.005$, ** $P < 0.01$, $^{ns}$ $P > 0.05$.

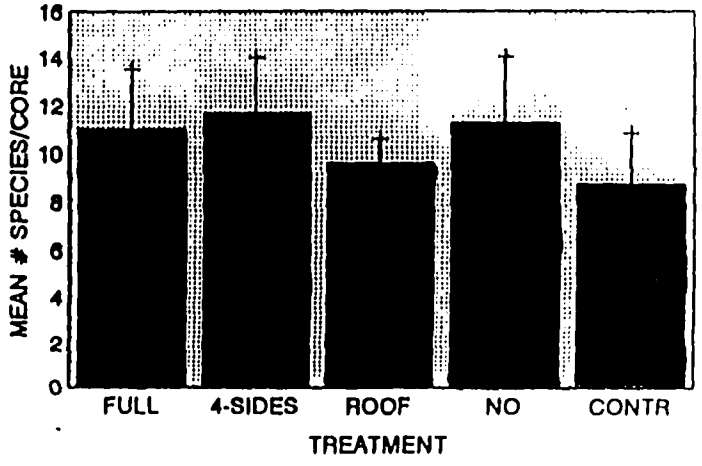
*2. Abundance differences for dominant species - Week 6*

Six weeks after cage deployment, some significant differences were found in diversity as well as individual species abundance when analyzed relative to river zone and caging treatment in the York River. Species richness (R) for the 6-week sampling in the York River was significantly greater downriver than upriver, though there were not significant differences between caging treatments (Fig. 2.4, Table 2.6a). Much of the variation was due to zone (44.9%). Greater diversity downriver was not surprising, as this trend has been seen in the literature (Remane and Schlieper 1971, Boesch 1977). Differences in H' and $\lambda$ were examined through time and will be discussed along with final results at week 12.

Abundance of dominant species (see Table 2.3) were compared by treatment six weeks after cage deployment (Fig. 2.5, Table 2.6b). Downriver, dominant infauna included five species of polychaetes, juveniles of the bivalve *Mercenaria mercenaria*, and some bivalves other than *Mercenaria*. 'Other' rare species were combined and also compared by treatment. There was extreme variation between replicate sites (high standard errors), thus few significant differences were detected. Four of five dominant polychaete species had greatest abundance in the 'full cage' treatment (Fig. 2.5). In all taxa, the 'full cage' treatment allowed higher abundances than the control, suggesting that removing predators may increase infaunal abundance at high salinity, but these trends were not significant after 6 weeks. Thus, predator exclusion can increase abundance in most species.

Fig. 2.4. Benthic species richness (mean # sp. per 0.006 $m^2$ core) for York River samples at 6-weeks after cage deployment (September 1993) for (a) Downriver and (b) Upriver zones. Each bar represents a different treatment, and the treatments are listed in order of increasing predator access. Compare bars on the left (low predation) to bars on the right (high predation).

## SPECIES RICHNESS
**DOWNRIVER**




## SPECIES RICHNESS
**UPRIVER**

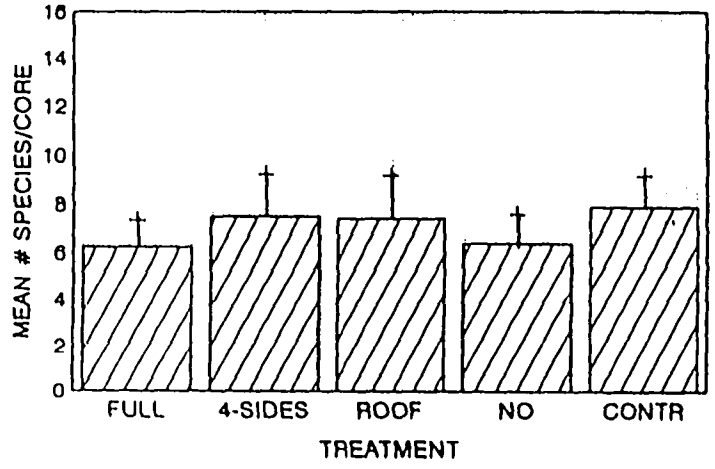
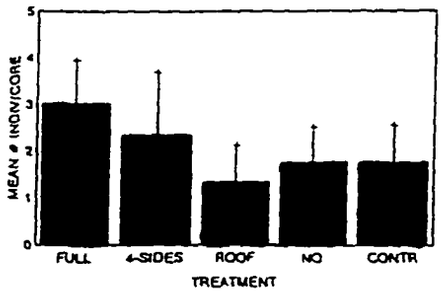
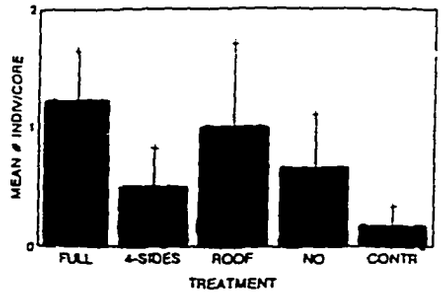


Fig. 2.5. Benthic abundance for eight dominant Downriver York taxa (Mean # individ./ 0.006 $m^2$ core $\pm$ SE) from four replicate sites. The treatments are listed in order of increasing predator access. Compare bars on the left (low predation) to bars on the right (high predation).

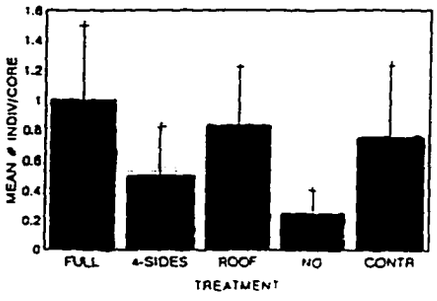
Nereis succinea



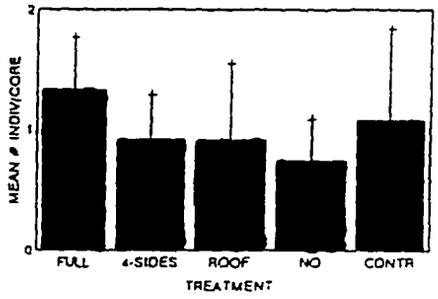

Gyptis vittata



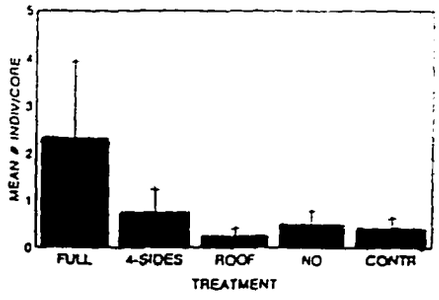

Heteromastus filiformis



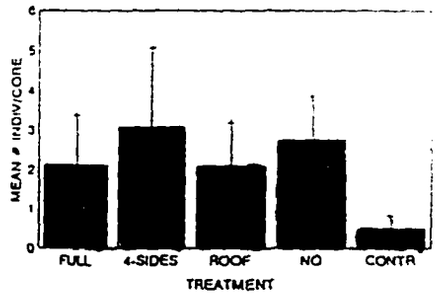

Other Bivalves



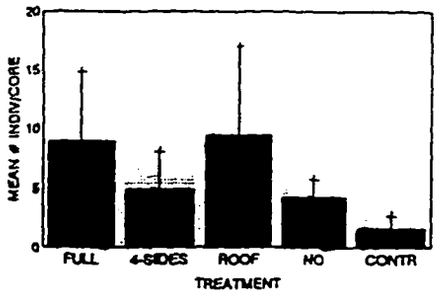

Tharyx sp.




Clymenella torquata




Mercenaria mercenaria




Others

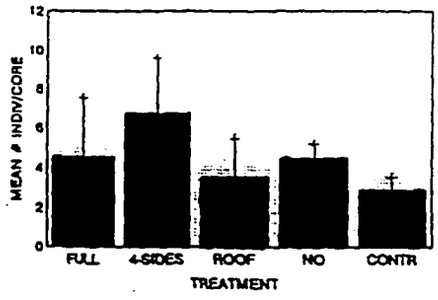


Table 2.6. (a) Benthic species richness at the **6-Week** sampling on the York River. ANOVA factors consisted of Cage type ('full cage', 'roof only', 'sides only', 'cage control' and 'no cage'), Zone (Downriver and Upriver), blocked by Site (four replicate sites in each zone).

| Diversity Measure | Source of variation | SS | df | MS | F |
|---|---|---|---|---|---|
| Richness (R) | Cage Type | 8.44 | 4 | 2.11 | $0.55^{ns}$ |
| | Zone | 113.91 | 1 | 113.91 | 29.74**** |
| | Cage x Zone | 25.56 | 4 | 6.39 | $1.67^{ns}$ |
| | Site | 2.31 | 3 | 0.77 | $0.20^{ns}$ |
| | Error | 103.43 | 27 | 3.83 | |
| | Total | 253.65 | 39 | | |

**** $P < 0.005$, *** $P < 0.005$, $^{ns}P > 0.05$.

Table 2.6. (b) Benthic abundance differences due to cage treatment **6 weeks** after cage deployment for the York River. ANOVA results for selected abundant infauna for both downriver and upriver zones. P = polychaete, O = oligochaete, B = bivalve. * = common to both river zones.

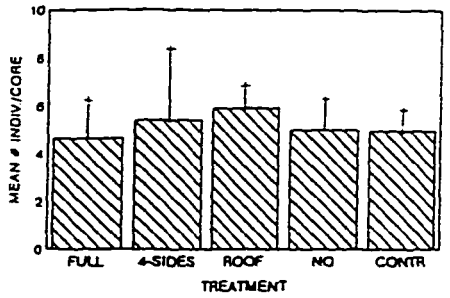
| Species | df | SS | F | *P* |
|---|---|---|---|---|
| **UPRIVER:** | | | | |
| *Streblospio benedicti* (P) | 4 | 44.2 | 1.2 | 0.34 |
| Tubificidae (O) | 4 | 146.7 | 36.7 | 0.21 |
| **DOWNRIVER:** | | | | |
| *Heteromastus filiformis* (P) * | 4 | 1.23 | 0.56 | 0.69 |
| *Tharyx* sp. (P) | 4 | 9.87 | 1.45 | 0.27 |
| *Nereis succinea* (P) | 4 | 1.29 | 0.08 | 0.99 |
| *Mercenaria mercenaria* (B) | 4 | 168.0 | 0.55 | 0.70 |

The extreme variation between sites probably contributed to a lack of detectable between-treatment differences for most species, thus a closer examination for some abundant species was necessary. I selected the most abundant infaunal species, juvenile *Mercenaria mercenaria*, and carefully compared abundance across replicate sites and treatments. Two sites had very low, one site had intermediate, and one site had high abundances. At the high abundance site (i.e., site 2, Downriver NW), I investigated the effect of caging on abundance. To get replication at that single site, I used the two time periods (week 6 and week 12) as replicates blocked by time. When analyzed in this way, there was a significant difference between treatments (ANOVA, df = 4, F = 8.41, $P$ = 0.031), whereby the 'full cage' treatment had high abundance, and the abundance within the 'roof only' cage was significantly higher than that in areas exposed to predators (e.g., 'cage control' and 'no cage'; Tukey test, Critical value, 5.67, $P < 0.05$). This suggests that only at high infaunal abundances is predation important, otherwise, the system may be driven by recruitment limitation. If the effect of predation can be seen only at high densities, infaunal densities of many species may be too low for detection of treatment effects in this study, or sample size was too low.

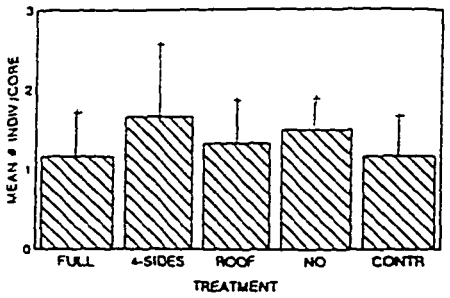
Upriver, at week 6, there were no significant differences in individual species abundance between treatments. The power was low (0.30 for oligochaetes, the species with closest significance) and sample size needed to detect a difference of 4.85 at 90% probability is 40 (Table 2.6b). Some trends in abundance due to caging, however, were apparent (Fig. 2.6). Various species showed elevated abundance within the 'full cage' compared to the 'no cage' or 'cage control' (e.g., *Streblospio benedicti*, *Macoma mitchelli*

Fig. 2.6. Benthic abundance for eight dominant Upriver York taxa (Mean # individ./ 0.006 $m^2$ core $\pm$ SE) from four replicate sites. The treatments are listed in order of increasing amount of predation. Compare bars on the left (low predation) to bars on the right (high predation).

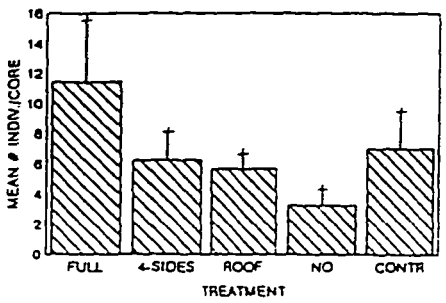
Nereis succinea



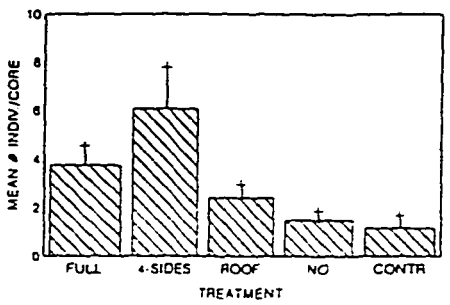

Glycinde solitaria



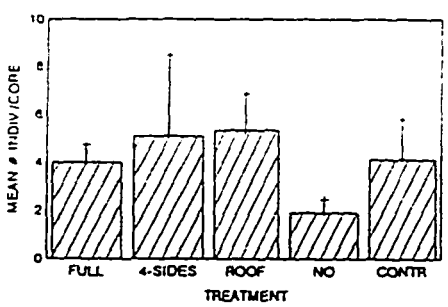

Oligochaetes



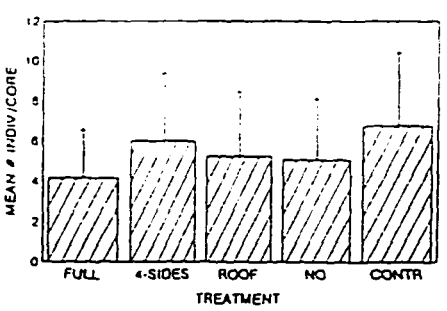

Streblospio benedicti



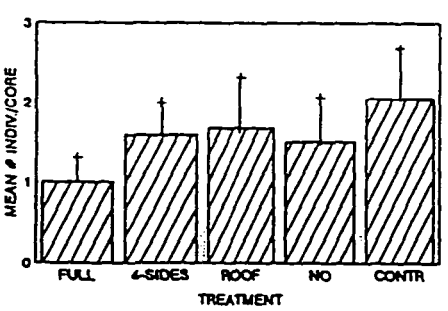

Macoma mitchelli



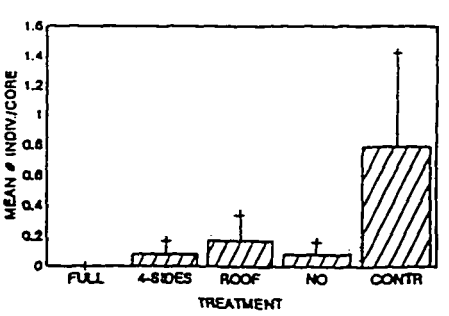

Heteromastus filiformis




Macoma balthica




Amphipoda



and Oligochaetes; Fig. 2.6). In contrast, some species showed no change or the opposite trend (*Nereis succinea*, *Heteromastus filiformis*, *Macoma balthica*, and all Amphipods combined; Fig. 2.6). Note that more amphipods were present at the 'cage control' treatment which provided structure for epifaunal species. At week 6, abundance of individual species were not significantly changed by predator exclusion or attraction (i.e., attraction to structure in the 'roof only' or 'cage control' treatment). The next level of investigation involved determination of diversity measures for all sites over both time periods, 6 and 12 weeks after the initial cage deployment.

### *3. Species diversity differences - Weeks 6 & 12*

Predation had a greater effect on benthic diversity upriver than downriver. Differences in diversity due to caging treatments was analyzed across sampling weeks 6 and 12 for both $1-\lambda$ and H'. Both diversity indices showed similar results, but varied slightly due to the different ways they calculate diversity.

#### *a. Simpson's diversity* ($1-\lambda$)

For Simpson's diversity, predation had a greater effect on diversity upriver. Downriver, diversity remained fairly constant from week 6 to week 12 (Fig. 2.7a); upriver, diversity in all treatments declined from week 6 to week 12 (Fig. 2.7b), apparently due to recruitment of some species, and a consequent reduction in evenness (see Appendix II). Diversity in the treatments with probable predator activity (e.g., 'roof only' and 'cage control') remained highest. A multi-way ANOVA revealed significant diversity differences

Fig. 2.7. Simpson's diversity values ($1-\lambda$) for the 'no cage' treatment at initial deployment (week 0), and for all cage treatments at 6 weeks and 12 weeks after deployment. (a) Downriver, (b) Upriver.

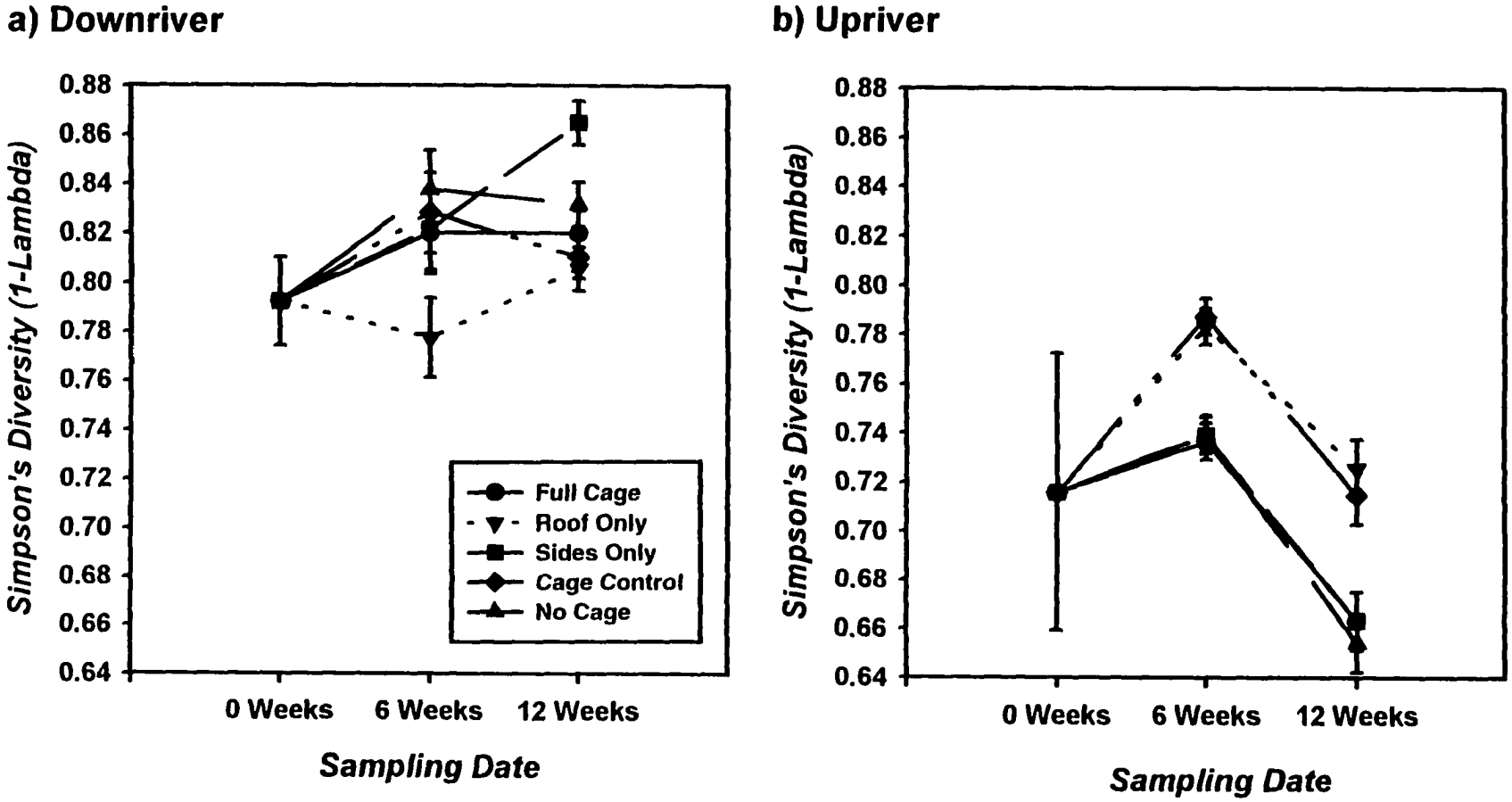


Table 2.7. Log-transformed Simpson's index (λ) across two sampling periods **6 and 12-Weeks** on the York River. ANOVA factors consisted of Cage type ('full cage', 'roof only', 'sides only', 'cage control' and 'no cage'), Zone (Downriver and Upriver), Time (week 6 and 12), blocked by Site (four replicate sites in each zone).

| Diversity Measure/Factor | Source of variation | SS | df | MS | F |
|---|---|---|---|---|---|
| (a) Simpson's Index (log λ)/ Downriver & Upriver | Cage Type | 0.071 | 4 | 0.018 | $0.47^{ns}$ |
| | Zone | 2.645 | 1 | 2.645 | 70.07**** |
| | Time | 12.635 | 1 | 12.635 | 334.74**** |
| | Cage x Zone | 0.365 | 4 | 0.091 | $2.42^{ns}$ |
| | Cage x Time | 0.067 | 4 | 0.017 | $0.44^{ns}$ |
| | Zone x Time | 0.996 | 1 | 0.996 | 26.37**** |
| | Cg x Zn x Tm | 0.150 | 4 | 0.038 | $0.99^{ns}$ |
| | Site | 0.168 | 3 | 0.056 | $1.49^{ns}$ |
| | Error | 2.152 | 57 | 0.038 | |
| | Total | 19.250 | 79 | | |
| (b) Downriver | Cage Type | 0.054 | 4 | 0.014 | $1.18^{ns}$ |
| | Time | 0.001 | 1 | 0.001 | $0.13^{ns}$ |
| | Cage x Time | 0.036 | 4 | 0.009 | $0.79^{ns}$ |
| | Site | 0.148 | 3 | 0.049 | 4.31* |
| | Error | 0.310 | 27 | 0.011 | |
| | Total | 0.550 | 39 | | |
| (c) Upriver | Cage Type | 0.079 | 4 | 0.019 | 3.09* |
| | Time | 0.104 | 1 | 0.104 | 16.40**** |
| | Cage x Time | 0.001 | 4 | 0.001 | $0.05^{ns}$ |
| | Site | 0.108 | 3 | 0.036 | 5.69*** |
| | Error | 0.171 | 27 | 0.006 | |
| | Total | 0.464 | 39 | | |

**** $P < 0.001$, *** $P < 0.005$, * $P < 0.05$, $^{ns}$ $P > 0.05$.

due to Zone and Time (Table 2.7a), but a significant Cage effect was only found upriver with a 2-way ANOVA (Table 2.7c). For λ, log-transformed data had homogeneous variance between river zones (Bartlett's test: T = 0.579, $P = 0.447$; Levene's test: T = 1.008, $P = 0.322$) and were used for comparisons, because raw data were heterogeneous (Bartlett's test: T = 11.25, $P = 0.001$; Levene's test: T = 6.43, $P = 0.015$). For the multi-way ANOVA, there was also a nearly significant (at alpha = 0.05) Cage x Zone interaction ($P = 0.059$). Because of this, to be conservative, each zone was analyzed separately.

Downriver, the only significant effects were for Site (Table 2.7b), but upriver a significant Cage effect was detected, as well significant Time and Site effects (Table 2.7c). Because of the significant Time x Zone interaction in the multi-way ANOVA, each time was run separately. Both time periods showed a significant Zone effect, as seen in the multi-way ANOVA. Thus, Simpson's diversity showed significant effects of predation only upriver, whereby the cages that allow most predator access (e.g., 'roof only') had significantly higher diversity than all other treatments (Tukey test, $P < 0.05$ for 'roof only' and 'cage control' compared to other treatments).

*b. Shannon-Wiener diversity (H')*

Downriver displayed far greater H' diversity than upriver (similar to results for λ), and river zone explained much of the total variation (51%). However, there were no significant Cage treatment effects for the multi-way ANOVA (Fig. 2.8; Table 2.8a). Variance between zones for H' was homogeneous, so raw data could be used for analysis (Bartlett's test: T = 0.028, $P = 0.867$; Levene's test: T = 0.004, $P = 0.95$). In the

Fig. 2.8. Shannon-Wiener species diversity values (bits per individual) for the 'no cage' treatment at initial deployment (week 0), and all cage treatments at 6 weeks and 12 weeks after deployment. (a) Downriver, (b) Upriver.

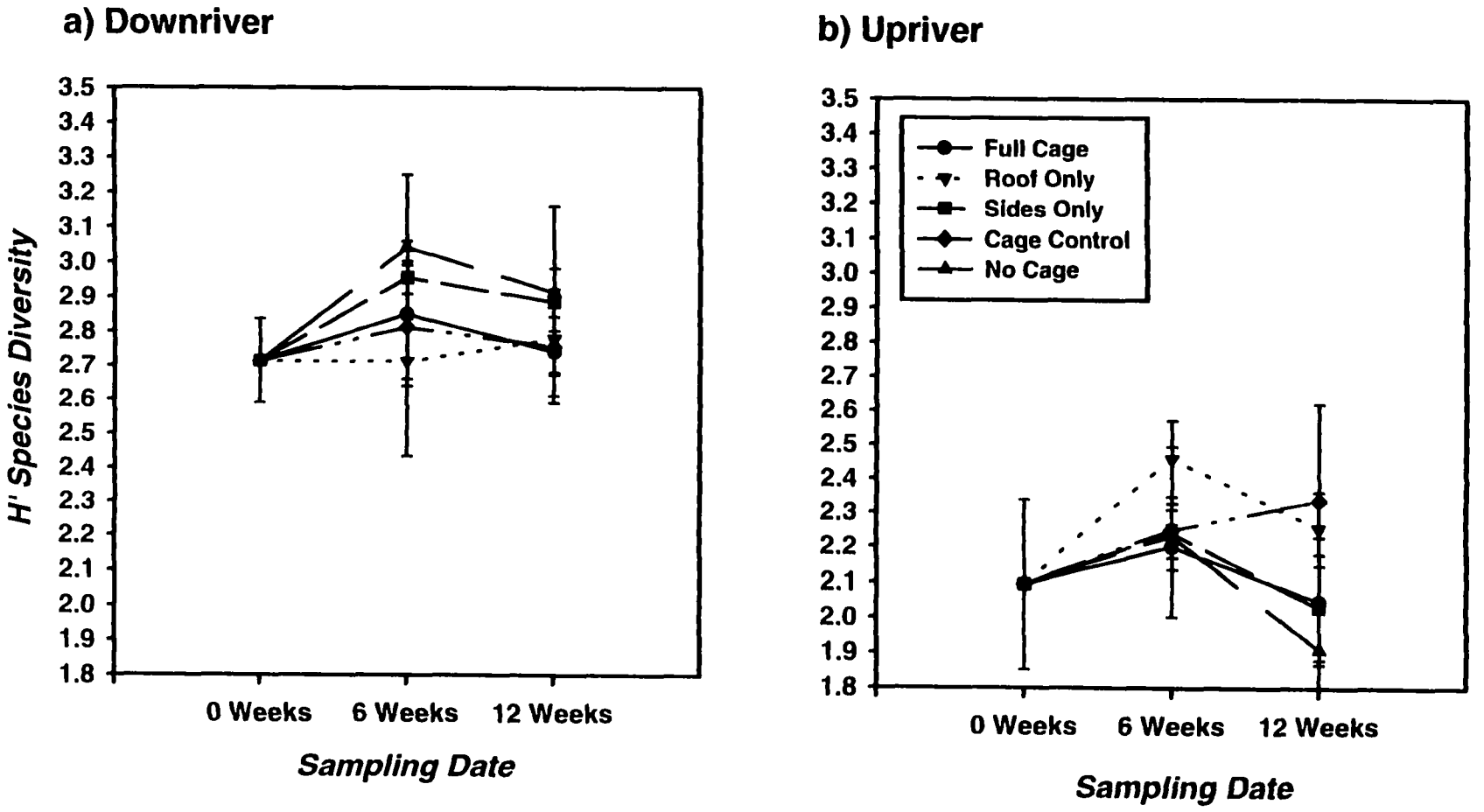


Table 2.8. Shannon-Wiener diversity (H') across two sampling periods **6 and 12-Weeks** on the York River. ANOVA factors consisted of Cage type ('full cage', 'roof only', 'sides only', 'cage control' and 'no cage'), Zone (Downriver and Upriver), Time (week 6 and 12), blocked by Site (four replicate sites in each zone).

| Diversity Measure/Factor | Source of variation | SS | df | MS | F |
|---|---|---|---|---|---|
| (a) Shannon-Wiener (H')/ Downriver & Upriver | Cage Type | 0.076 | 4 | 0.019 | $0.17^{ns}$ |
| | Zone | 8.450 | 1 | 8.450 | 76.63**** |
| | Time | 0.246 | 1 | 0.246 | $2.23^{ns}$ |
| | Cage x Zone | 0.715 | 4 | 0.176 | $1.62^{ns}$ |
| | Cage x Time | 0.128 | 4 | 0.032 | $0.29^{ns}$ |
| | Zone x Time | 0.050 | 1 | 0.050 | $0.45^{ns}$ |
| | Cg x Zn x Tm | 0.102 | 4 | 0.026 | $0.23^{ns}$ |
| | Site | 0.518 | 3 | 0.173 | $1.57^{ns}$ |
| | Error | 6.285 | 57 | 0.110 | |
| | Total | 16.570 | 79 | | |
| (b) Downriver | Cage Type | 0.313 | 4 | 0.078 | $0.63^{ns}$ |
| | Time | 0.037 | 1 | 0.037 | $0.30^{ns}$ |
| | Cage x Time | 0.047 | 4 | 0.012 | $0.09^{ns}$ |
| | Site | 0.405 | 3 | 0.135 | $1.08^{ns}$ |
| | Error | 3.368 | 27 | 0.125 | |
| | Total | 4.170 | 39 | | |
| (c) Upriver | Cage Type | 0.479 | 4 | 0.120 | $1.46^{ns}$ |
| | Time | 0.258 | 1 | 0.258 | $3.15^{ns}$ |
| | Cage x Time | 0.183 | 4 | 0.046 | $0.56^{ns}$ |
| | Site | 0.821 | 3 | 0.274 | 3.34* |
| | Error | 2.209 | 27 | 0.018 | |
| | Total | 3.951 | 39 | | |

* $P < 0.05$, $^{ns}P > 0.05$.

ANOVA, the Cage x Zone interaction was nearly significant and power was low (due to low sample size), therefore 2-way ANOVAs were conducted for each Zone separately.

Analyses for H' in the two zones separately revealed no significant differences downriver (Table 2.8b) but some upriver (Table 2.8c). Upriver across both time periods, there was no Cage effect, a significant Site effect (explaining 21% of the variation), and a nearly significant Time effect (Table 2.8c). To be conservative, I analyzed each time period separately.

At 6 weeks, there were no significant differences due to Cage treatment either downriver (ANOVA, df = 19, MS = 0.065, F = 0.51, $P = 0.73$), or upriver (ANOVA, df = 19, MS = 0.043, F = 0.54, $P = 0.71$). But at 12 weeks upriver, significant differences in species diversity due to Cage treatment (ANOVA, df = 19, MS = 0.122, F = 4.58, $P = 0.02$), and Site (MS = 0.540, F = 20.24, $P = 0.001$) were detected. The 'roof only' and 'cage control' treatments had significantly higher diversity than other treatments (Tukey test, $P < 0.05$). Downriver at 12-weeks, there was no effect of caging (ANOVA, df = 19, MS = 0.025, F = 0.25, $P = 0.90$). Thus, for H', the only effect of predation on benthic diversity was seen upriver. Diversity was highest in caging treatments where predator access was greatest, suggesting that predation maintains diversity.

### *4. Changes in Richness, Evenness and Abundance - Week 12*

Diversity encompasses both richness and evenness, thus, to discern the mechanisms behind the shifts in diversity upriver, I further examined species richness,

evenness and abundance for the different treatments after 12 weeks of cage deployment. None of these parameters alone showed significant effects due to caging, but a combination of these factors helped explain the cause of diversity shifts. Richness increased slightly with increased predator access (Fig. 2.9a, b); upriver there was higher richness in the 'roof only' and 'cage control' treatments (with high richness also in 'full cage'), though this effect was not significantly different downriver or upriver (Table 2.9a, b). Evenness downriver and upriver showed a similar pattern with cage treatment (Fig. 2.9c, d); evenness was highest in the cage treatments where predators had greatest access (e.g., 'roof only', 'cage control' and 'no cage') though this was not significant (Table 2.9c, d). Abundance of individuals may affect evenness if there is recruitment of a few individuals. There was not much difference in abundance with treatment downriver (Fig. 2.9e), but upriver, abundance increased substantially and was highest where predators were excluded (e.g., the 'full cage'; Fig. 2.9f), though the differences were not significant (Table 2.9d, f). Thus, upriver, the increased diversity in cages with predator access (e.g., 'roof only' and 'cage control') derived most notably from increased evenness, slightly increased richness along with decreased abundance.

To summarize, downriver, there was no significant difference in $1-\lambda$ or H' diversity due to treatment. Downriver, the number of individuals did not change considerably from 6 to 12 weeks (compare Fig. 2.3a with 2.9e), indicating that recruitment was low. In contrast, upriver, there was a significant difference due to treatment for Simpson's diversity (across weeks 6 and 12) and H' (only seen at week 12). Upriver, abundance increased in cages with predator exclusion (e.g., 'full cage'; compare Fig. 2.3b with 2.9f),

Fig. 2.9. Benthic species richness (a) Downriver and (b) Upriver, Evenness (c) Downriver and (d) Upriver, Abundance (e) Downriver and (f) Upriver in York at 12 weeks sampling.

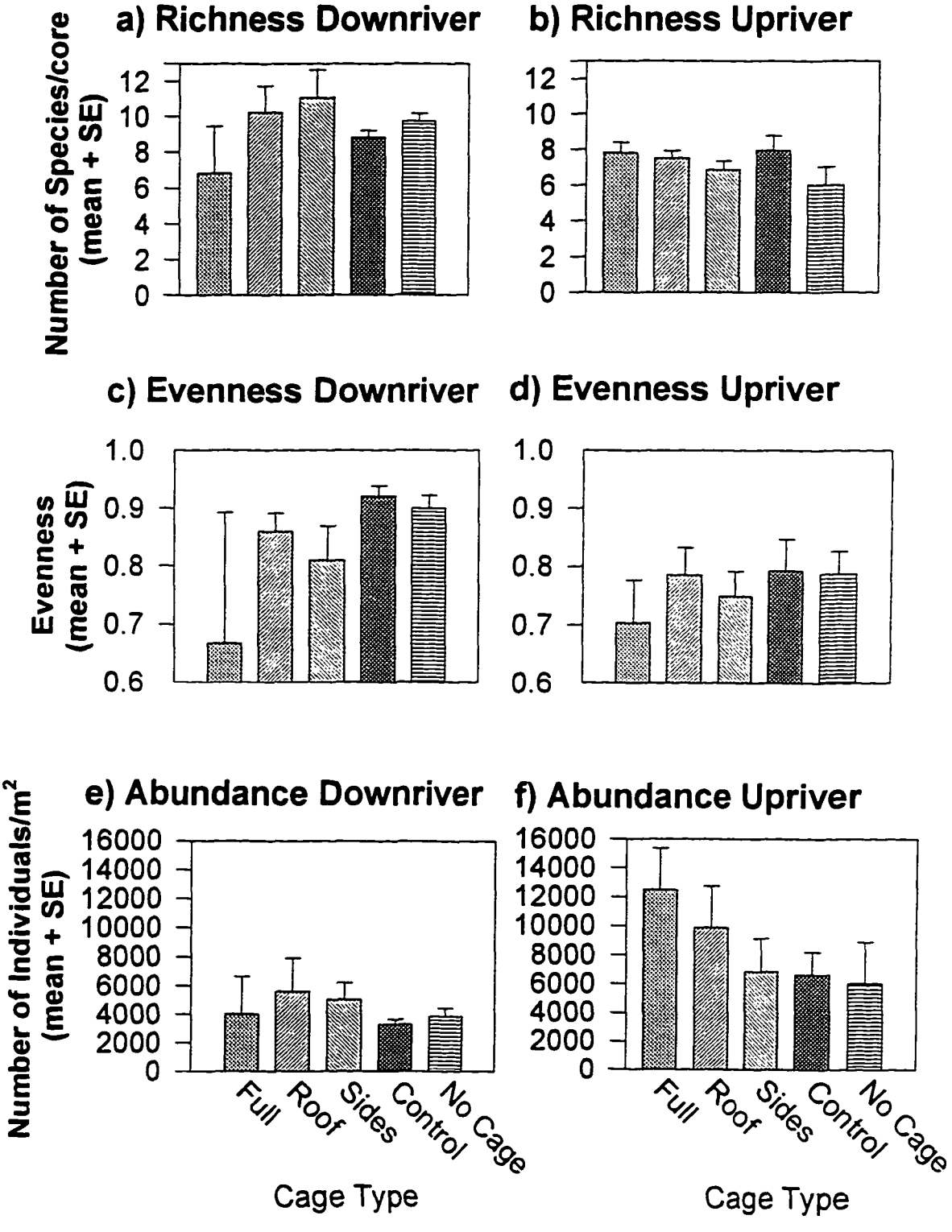


Table 2.9. Richness, Evenness and Abundance for each river zone separately (1-way ANOVAs blocked by site) in the York.

a. Analysis of Variance for Mean Richness Downriver

| Source | DF | Seq SS | Adj SS | Adj MS | F | P |
|---|---|---|---|---|---|---|
| cage type | 4 | 42.302 | 42.302 | 10.576 | 1.77 | 0.200 |
| site | 3 | 70.777 | 70.777 | 23.592 | 3.95 | 0.036 |
| Error | 12 | 71.741 | 71.741 | 5.978 | | |
| Total | 19 | 184.821 | | | | |

b. Analysis of Variance for Mean Richness Upriver

| Source | DF | Seq SS | Adj SS | Adj MS | F | P |
|---|---|---|---|---|---|---|
| cage type | 4 | 10.302 | 10.302 | 2.576 | 1.98 | 0.162 |
| site | 3 | 13.898 | 13.898 | 4.633 | 3.55 | 0.048 |
| Error | 12 | 15.639 | 15.639 | 1.303 | | |
| Total | 19 | 39.839 | | | | |

c. Analysis of Variance for Mean Evenness Downriver

| Source | DF | Seq SS | Adj SS | Adj MS | F | P |
|---|---|---|---|---|---|---|
| cage type | 4 | 0.16324 | 0.16324 | 0.04081 | 1.00 | 0.445 |
| site | 3 | 0.18278 | 0.18278 | 0.06093 | 1.49 | 0.266 |
| Error | 12 | 0.48926 | 0.48926 | 0.04077 | | |
| Total | 19 | 0.83528 | | | | |

d. Analysis of Variance for Mean Evenness Upriver

| Source | DF | Seq SS | Adj SS | Adj MS | F | P |
|---|---|---|---|---|---|---|
| cage type | 4 | 0.022770 | 0.022770 | 0.005693 | 1.03 | 0.432 |
| site | 3 | 0.098885 | 0.098885 | 0.032962 | 5.96 | 0.010 |
| Error | 12 | 0.066415 | 0.066415 | 0.005535 | | |
| Total | 19 | 0.188070 | | | | |

e. Analysis of Variance for Mean Abundance Downriver

| Source | DF | Seq SS | Adj SS | Adj MS | F | P |
|---|---|---|---|---|---|---|
| cage type | 4 | 502.1 | 502.1 | 125.5 | 0.58 | 0.680 |
| site | 3 | 3386.0 | 3386.0 | 1128.7 | 5.26 | 0.015 |
| Error | 12 | 2575.5 | 2575.5 | 214.6 | | |
| Total | 19 | 6463.7 | | | | |

f. Analysis of Variance for Mean Abundance Upriver

| Source | DF | Seq SS | Adj SS | Adj MS | F | P |
|---|---|---|---|---|---|---|
| cage type | 4 | 4326.1 | 4326.1 | 1081.5 | 1.49 | 0.266 |
| site | 3 | 5052.7 | 5052.7 | 1684.2 | 2.32 | 0.127 |
| Error | 12 | 8698.2 | 8698.2 | 724.9 | | |
| Total | 19 | 18077.0 | | | | |

resulting in decreased evenness (Fig. 2.9d) and thus lower diversity there. Recruitment was apparently higher upriver, and diversity was highest where new recruits were consumed by predators (e.g., 'roof only' and 'cage control' treatments). Recruitment has been demonstrated to set the structure of macrobenthic communities. Following recruitment pulses, intense predation by fish and crabs can reduce infaunal abundances (Holland et al. 1985). Reduced abundances of new recruits would lead to increased evenness.

The elevation in evenness upriver in cages where predators were attracted (e.g., 'roof only' and 'cage control') is plausible because the predators could crop the abundant infauna, not allowing any one species to become dominant. Also of note is the reduced diversity from 6 to 12 weeks for all treatments (Figs. 2.7 and 2.8). Across time periods the richness remained approximately equal, but the abundance of some species increased, thus evenness was reduced substantially. Upriver, recruitment (evidenced by increased abundance) occurred in all treatments, but in treatments with elevated predator density, new recruits were cropped, keeping evenness high (resulting in high H' and $1-\lambda$). These infaunal results suggest that predators are most active in the 'roof only' and 'cage control' treatments. To corroborate this hypothesis, the predation activity in each cage type and the abundance of predators in each zone were quantified.

## II. CAGING ARTIFACTS & EFFECTS

### A. Predator Behavior

When caging manipulations are used and significant effects are established, it is necessary to confirm the effects by looking at the cage efficiency. In the York River system, visibility is poor, thus efficiency of cages was determined in large mesocosms in the laboratory where predator activity around the cages could be established. Movements of predators in and around each of the five cage types in a 2-hour period were quantified to estimate probable movement around cages and access by predators to the benthos within the cages in the field.

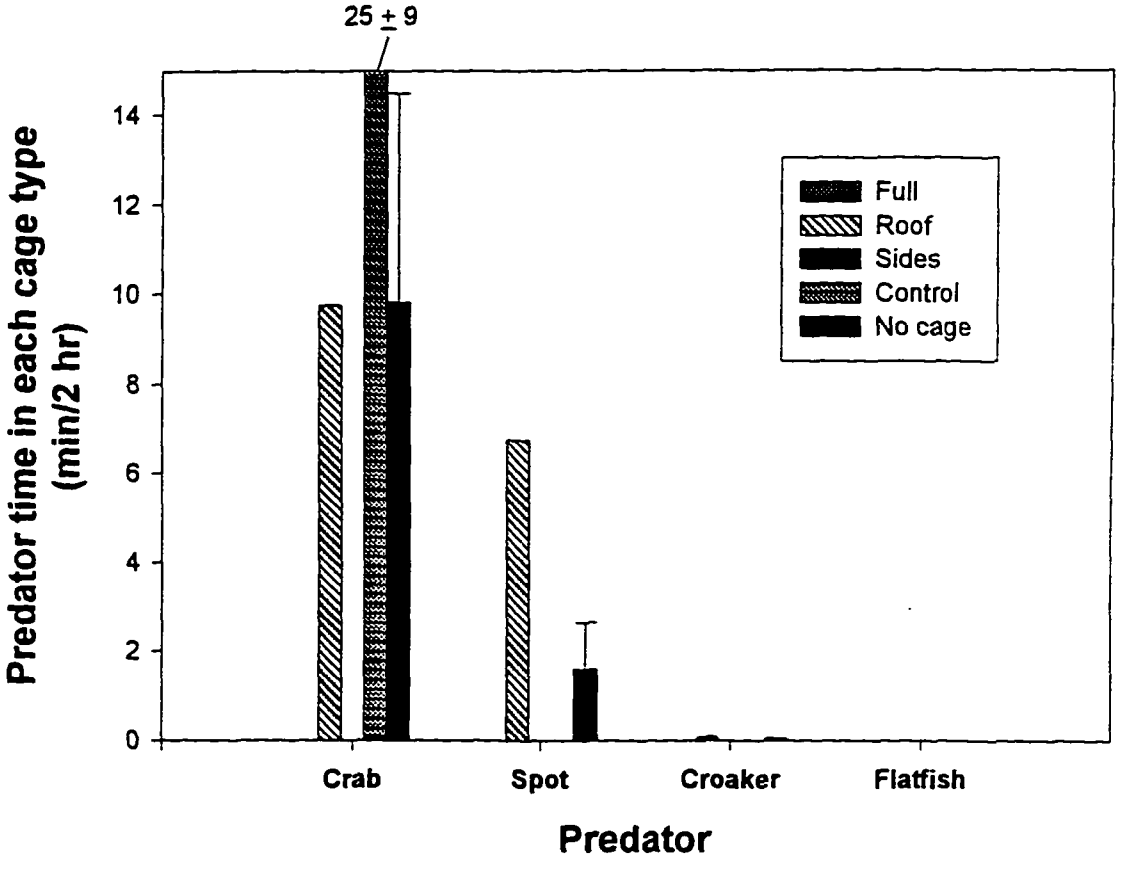
A comparison of time spent in each cage by each predator showed a significant Predator effect, a significant Cage treatment effect, and a Predator x Cage interaction (Table 2.10a). Crabs were the most active predator in cages (mean of 9 min/trial across all cage types) though spot were also active (mean of 1.1 min/trial across all cage types), and croaker were slightly active (mean of 0.02 min/trial across all cage types; Fig. 2.10). In addition, the 'cage control' treatment had highest predator activity within it (mean of 10.17 min/trial for all predators), the 'roof only' treatment had second highest activity (mean of 3.84 min/trial for all predators), then the 'no cage' treatment (mean of 2.86 min/trial for all predators). Both treatments with notable access by predators (e.g., 'cage control' and 'roof only') had higher predator activity than the 'no cage' (i.e., natural sediment) treatment, suggesting that these cages attracted predators, rather than excluding them somewhat. The 'sides only' treatment had no activity within it, which may have been a consequence of the water depth in the mesocosms; the water was only 25 cm above the

Table 2.10a. Predator behavior in GEM lab experiments comparing time spent (over a total of 2 hours) in each cage type by each of four predator groups. ANOVA factors consisted of Cage type ('full cage', 'roof only', 'sides only', 'cage control' and 'no cage'), and Predator including the blue crab *Callinectes sapidus*, spot *Leiostomus xanthurus*, croaker *Micropogonias undulatus*, and a flatfish (either hogchoker *Trinectes maculatus*, or summer flounder *Paralychthes dentatus*).

A 3-way analysis of Variance for time spent in each cage (min) by predator

| Source | DF | Seq SS | Adj SS | Adj MS | F | P |
|---|---|---|---|---|---|---|
| predator | 3 | 544.10 | 521.88 | 173.96 | 14.82 | 0.000 |
| cage type | 4 | 316.51 | 183.97 | 45.99 | 3.92 | 0.021 |
| pred*cage | 12 | 588.53 | 588.53 | 49.04 | 4.18 | 0.005 |
| Error | 16 | 187.83 | 187.83 | 11.74 | | |
| Total | 35 | 1636.96 | | | | |

Fig. 2.10. Mean time in minutes spent in each cage treatment ('full cage', 'roof only', 'sides only', 'cage control' and 'no cage') by each of 4 predator taxa (Blue crabs, spot, croaker, or flatfish) from behavioral experiments in the GEM laboratory.



cage top. This water level, however is similar to that in which cages were placed in the field, and therefore may indicate that these cages were not accessed by predators in the field either. Note that bait was added to the cages, so the recorded activity within the 2 hour trial was a liberal estimate of predator activity.

One-way ANOVAs for each predator and cage were run because of the Predator x Cage interaction (only for those predators that showed any activity, and only for cages that predators used). For blue crabs, there was significantly more time spent in the 'cage control' versus the 'full cage' or 'sides only' treatment (Tukey pairwise comparison, $P < 0.05$), and much time was also spent in the 'roof only' and 'no cage' treatments (though not significantly different from 'full cage' or 'sides only', Tukey pairwise comparison, $P > 0.05$; Table 2.10b). For spot, significantly more time was spent in the 'roof only' treatment compared to all other treatments (Tukey pairwise comparison, $P< 0.05$; Table 2.10b). For croaker, there was no significant difference in time spent in the different cages, though some minimal time was spent in both the 'roof only' and 'no cage' treatments (Tukey pairwise comparison, $P >0.05$; Table 2.10b; Fig. 2.10).

Each cage type was analyzed separately, and there was significantly more time spent in 'roof only' by crabs than spot or croaker, and significantly more time spent by spot than croaker (Table 2.10b). In the 'cage control' and 'no cage', there was no significant difference in the amount of time spent by each predator of those that used the cage at all (Table 2.10b). This suggests that both the 'cage control' and 'no cage' are used somewhat by all predators, but the 'roof only' is used more by crabs than any other predators. Thus, any differences in infaunal densities in the 'roof only' treatment are primarily due to crab

Table 2.10b. Predator behavior in GEM lab experiments comparing time spent in each cage type by each of three predators separately, and each of three cage types separately (1-way ANOVAs). Predators compared were the blue crab *Callinectes sapidus*, spot *Leiostomus xanthurus*, and croaker *Micropogonias undulatus*. (the flatfish both hogchoker *Trinectes maculatus*, and summer flounder *Paralychthes dentatus* were not active in cages at all and were thus left out of 1-way ANOVAs). Cage types used were 'roof only', 'cage control', and 'no cage' ('sides only' and 'full cage' had no predator activity within them and were therefore not used in 1-way ANOVAs).

Analysis of Variance on time spent by crabs in each cage (min/24hr)

| Source | DF | SS | MS | F | p |
|---|---|---|---|---|---|
| Cage type | 4 | 866.6 | 216.6 | 5.84 | 0.040 |
| Error | 5 | 185.5 | 37.1 | | |
| Total | 9 | 1052.1 | | | |

Analysis of Variance on time spent by spot in each cage (min/24hr)

| Source | DF | SS | MS | F | p |
|---|---|---|---|---|---|
| Cage type | 4 | 39.838 | 9.960 | 17.51 | 0.008 |
| Error | 4 | 2.276 | 0.569 | | |
| Total | 8 | 42.114 | | | |

Analysis of Variance on time spent by croaker in each cage (min/24hr)

| Source | DF | SS | MS | F | p |
|---|---|---|---|---|---|
| Cage type | 4 | 0.00344 | 0.00086 | 0.76 | 0.595 |
| Error | 5 | 0.00569 | 0.00114 | | |
| Total | 9 | 0.00914 | | | |

Analysis of Variance on Time spent by each predator in the Roof trt.

| Source | DF | SS | MS | F | p |
|---|---|---|---|---|---|
| Predator | 2 | 97.05175 | 48.52588 | 2.4E+04 | 0.000 |
| Error | 2 | 0.00403 | 0.00201 | | |
| Total | 4 | 97.05578 | | | |

Analysis of Variance on Time spent by each predator in the cage control trt.

| Source | DF | SS | MS | F | p |
|---|---|---|---|---|---|
| Predator | 2 | 647 | 323 | 2.28 | 0.424 |
| Error | 1 | 142 | 142 | | |
| Total | 3 | 789 | | | |

Analysis of Variance on Time spent by each predator in the no cage treatment

| Source | DF | SS | MS | F | p |
|---|---|---|---|---|---|
| Predator | 2 | 110.6 | 55.3 | 3.60 | 0.160 |
| Error | 3 | 46.1 | 15.4 | | |
| Total | 5 | 156.7 | | | |

activity, while differences in the 'cage control' and 'no cage' are attributable to crabs, spot and croaker alike. Although conditions in the lab are not identical to the field (i.e., no scouring or other current-induced compromises), the 'full cage' was effective in keeping predators out. This laboratory evidence supports field benthic diversity data showing a larger effect of predators in the 'roof only' and 'cage control' treatments.

**B. Sediment Effects** (grain size, carbon and nitrogen levels),

Although sediment type at all sites varied, all could be characterized as muddy sand. I attempted to establish the experimental sites in locations with approximately similar sediment types. In shallow water, sediments in the York are typically sandy or muddy-sand. The sediment grain-size analysis yielded percent gravel, sand, and fines (silt and clay) for each cage at each site; mean percentage of each size fraction (for 4 replicate sites) for each cage type in each zone between two time periods (initial deployment vs. 12 weeks) was compared with ANOVA.

In general, the cages did not significantly affect the sediments within, but there was a significant difference due to river Zone. There was no Cage x Time interaction, showing that predator exclusion cages had no greater change in sediment content than uncaged areas (Table 2.11a). This is encouraging and suggests that any differences in benthic diversity within the cages was not due to sediment deposition associated with the physical presence of the cage, but was instead due to the abundance of predators. There were no differences in the gravel fraction for any factors (most sites had no gravel), but significant differences were found in both the sand and silt/clay fractions for river zone (Table 2.11a).

Table 2.11a. Sediment analysis between time period 0 and week 12 (at initial deployment and after 12 weeks in the field). Factors included Cage type ('full cage', 'roof only', 'sides only', 'cage control' and 'no cage')Zone (Downriver, Upriver), and Time with Site as a blocking factor.

Analysis of Variance for sand

| Source | DF | Seq SS | Adj SS | Adj MS | F | P |
|---|---|---|---|---|---|---|
| cage type | 4 | 21.24 | 32.21 | 8.05 | 0.19 | 0.943 |
| Zone | 1 | 1594.34 | 1625.70 | 1625.70 | 38.39 | 0.000 |
| time | 1 | 2218.98 | 2134.40 | 2134.40 | 50.40 | 0.000 |
| cage*Zone | 4 | 70.95 | 71.77 | 17.94 | 0.42 | 0.791 |
| cage*time | 4 | 100.31 | 81.44 | 20.36 | 0.48 | 0.750 |
| Zone*time | 1 | 257.02 | 253.63 | 253.63 | 5.99 | 0.018 |
| cage*Zone*time | 4 | 116.05 | 127.72 | 31.93 | 0.75 | 0.560 |
| site | 3 | 630.26 | 630.26 | 210.09 | 4.96 | 0.004 |
| Error | 55 | 2328.98 | 2328.98 | 42.35 | | |
| Total | 77 | 7338.13 | | | | |

Analysis of Variance for silt & clay

| Source | DF | Seq SS | Adj SS | Adj MS | F | P |
|---|---|---|---|---|---|---|
| cage type | 4 | 20.78 | 29.78 | 7.44 | 0.18 | 0.946 |
| Zone | 1 | 1544.29 | 1575.13 | 1575.13 | 38.64 | 0.000 |
| time | 1 | 2188.24 | 2104.93 | 2104.93 | 51.64 | 0.000 |
| cage*Zone | 4 | 77.48 | 77.83 | 19.46 | 0.48 | 0.752 |
| cage*time | 4 | 104.23 | 85.05 | 21.26 | 0.52 | 0.720 |
| Zone*time | 1 | 237.63 | 233.97 | 233.97 | 5.74 | 0.020 |
| cage*zone*time | 4 | 112.55 | 125.14 | 31.29 | 0.77 | 0.551 |
| site | 3 | 614.01 | 614.01 | 204.67 | 5.02 | 0.004 |
| Error | 55 | 2242.00 | 2242.00 | 40.76 | | |
| Total | 77 | 7141.22 | | | | |

Table 2.11b. Mean percent sand and silt clay (with pooled SD) from 4 replicate sites for each cage pooled for both time periods (initial deployment and 12 weeks later).

Downriver

| Cage Type | Mean sand | Std. Dev. | Mean silt & clay | Std.Dev. |
|---|---|---|---|---|
| Full cage | 88.01 | 2.494 | 11.988 | 2.447 |
| Roof only | 87.28 | 2.301 | 12.706 | 2.257 |
| Sides only | 87.33 | 2.301 | 12.660 | 2.257 |
| Cage control | 86.37 | 2.301 | 13.616 | 2.257 |
| No cage | 88.30 | 2.301 | 11.420 | 2.257 |

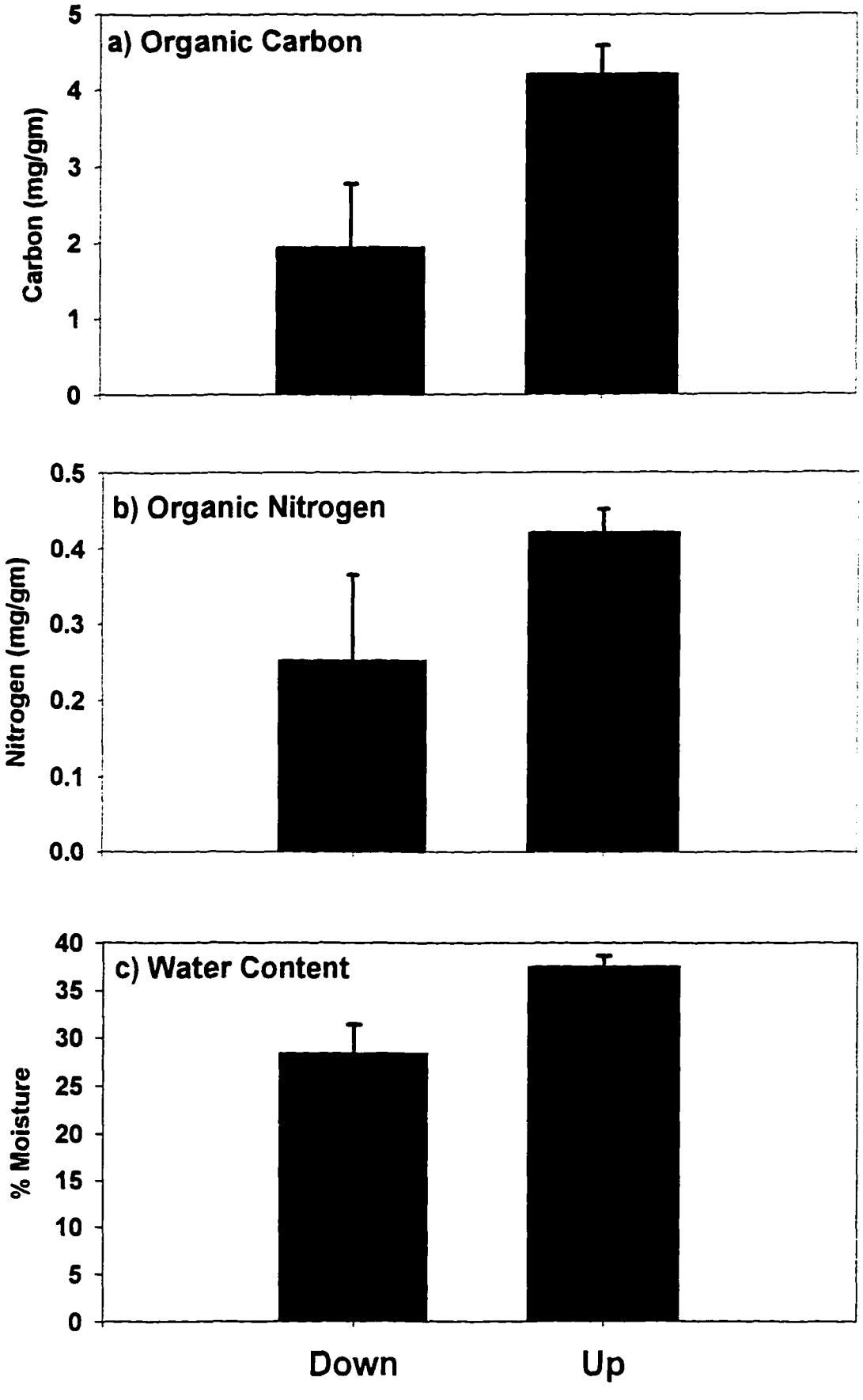
Upriver

| Cage Type | Mean | Std. Dev. | Mean silt & clay | Std.Dev. |
|---|---|---|---|---|
| Full cage | 79.93 | 2.301 | 19.878 | 2.257 |
| Roof only | 77.54 | 2.301 | 22.001 | 2.257 |
| Sides only | 77.37 | 2.301 | 22.554 | 2.257 |
| Cage control | 80.19 | 2.301 | 19.641 | 2.257 |
| No cage | 76.38 | 2.494 | 23.475 | 2.447 |

The percent sand was significantly higher (and silt & clay lower) downriver than upriver for all cage types. Percent sand was also higher for 12 weeks after deployment, compared to time 0 (Table 2.11b). The increased silt & clay fraction upriver was probably related to increased runoff and associated fine particulates from upriver.

The caging treatments produced no differences in organic nutrients, but there were significant differences due to river zone for organic carbon, organic nitrogen and water content. Upriver, concentrations of carbon were significantly greater than downriver (ANOVA, df = 9, F = 12.8, $P = 0.037$; Fig. 2.11a). Additionally, the C:N ratio, which can be an indicator of food quality (Valiela 1984), was approximately 10:1 upriver and 8:1 downriver, again indicating that upriver may have higher food quality. Concentrations of nitrogen, an element necessary for cell division and growth, were higher upriver than downriver, though not significantly so (ANOVA, df = 9, F = 2.12, $P = 0.183$); Fig. 2.11b). Higher upriver nutrient concentrations were likely because sites in this zone were closer to sources of carbon fixation such as tidal wetlands than downriver sites. Water content of the sediment was significantly higher upriver also (ANOVA, df = 9, F = 8.30, $P = 0.020$; Fig. 2.11c). None of these variables, however, varied with cage treatment (carbon by cage ANOVA, df = 0, F = 0.81, $P = 0.57$, nitrogen by cage ANOVA, df = 9, F = 1.36, $P = 0.367$; % water content by cage ANOVA, df = 9, F = 0.54, $P = 0.718$). This suggests that there were not any detectable sedimentary artifacts and that differences between cages was due to the abundance of predators, not the physical presence of the cage.

Fig. 2.11. Mean nutrient content for upriver and downriver sites for (a) organic carbon, (b) organic nitrogen, and (c) water content of the sediment.



## III. NATURAL PREDATOR ABUNDANCE

Natural epibenthic predator abundance in two zones in two rivers throughout three months of the summer predation period (late May, early July and early August) in 1994 were compared (pelagic predators caught in the trawl were not included). In Chesapeake Bay, dominant epibenthic predators include the blue crab as well as various demersal fishes (Horwitz 1987, Hines et al. 1990). The abundance and size-frequency distribution of predators in the shallow water areas of the York and Rappahannock Rivers (1-2 m depths) allow a unique look at shallow water predator abundance and distribution, with potential for comparison with deep water areas that are well studied (Mansour 1992, Holland et al. 1980, Lipcius and van Engel 1990).

Epibenthic predators caught in the York and Rappahannock Rivers included blue crabs (*Callinectes sapidus* Rathbun), spot (*Leiostomus xanthurus* Lacepede), and hogchoker (*Trinectes maculatus* Bloch and Schneider). Of the 6,605 predators caught, spot were most abundant and accounted for 46.22% numerically, hogchoker accounted for 20.08%, blue crabs accounted for 9.74%, and *Morone americana* in the Rappahannock accounted for 10.33%. The predator guild was mainly the same in the York and Rappahannock, with the addition of the perch, *Morone americana*, in the Rappahannock. Other predators included croaker (*Micropogonias undulatus*), summer flounder (*Paralichthys dentatus*), oyster toadfish (*Opsanus tau*), blue catfish, channel catfish, sea robin and lizardfish.

Epibenthic predators had entered the York and Rappahannock Rivers by May 1994 and were still present through August. The mean number of epibenthic predators

(bottom-feeding fish plus crabs) was significantly greater upriver than downriver across both rivers (Fig. 2.12a, b; Table 2.12a) and was significantly greater in late May (mean of 297.6 ± 69.5/4 minute trawl) than both July (mean 58.1 ± 16.8) and August (mean 57.1 ± 13.4; Tukey multiple comparison, critical value 3.43, $F = 10.89$, $P < 0.001$). There was no significant difference in the total number of fish predators between rivers, and all sites on at each river zone showed a similar pattern. There were significantly more epibenthic fish upriver than downriver and significantly more fish in May than July or August (Table 2.12b; Fig. 2.12a, b).

Looking at each major predator separately, the total number of crabs differed significantly by river zone as well as river and there was a significant River x Zone interaction (Table 2.12c; Fig. 2.12c, d). Because of the River x Zone interaction, one-way ANOVAs were run for crab abundance in each river separately (Table 2.12d, e). In the York River there were significantly more crabs upriver than downriver (Fig. 2.12c; Table 2.12d), but in the Rappahannock, there were few crabs overall, and there was no difference in the number of crabs found upriver or downriver (Fig. 2.12d; Table 2.12e). The number of spot did not differ by river or by river zone, although more were caught in May compared to July or August (Table 2.12f). There were also significantly more hogchoker upriver than downriver in the York, though few were collected in the Rappahannock (Table 2.12g, h, i). Although the trawling was not conducted in the same year as the caging experiments, similarities in seasonal water temperatures between years would allow similar patterns to occur annually. These significantly different abundances of

Fig. 2.12. Mean predator abundance (No. individuals) per 4-minute trawl from 4 replicate sites comparing downriver and upriver zones over the three approximately monthly samples in late May, early July and early August. (a) Epibenthic fish in the York, (b) epibenthic fish in the Rappahannock, (c) blue crabs in the York and (d) blue crabs in the Rappahannock River. Note that the y-axes are different for fish and crabs to display the maximum for each predator group.

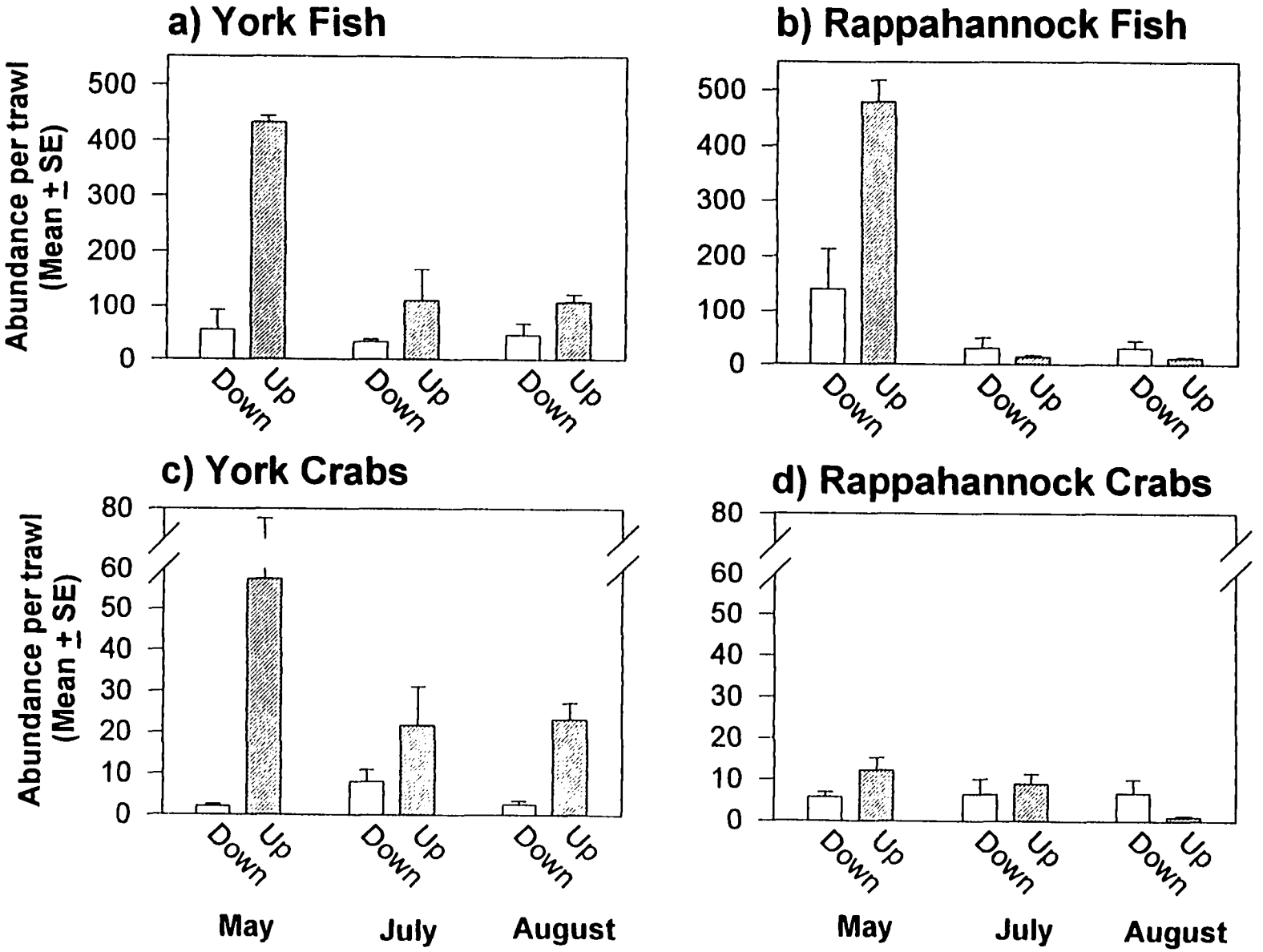


Table 2.12. Epibenthic predator abundance by River (York and Rappahannock) Zone (Downriver and Upriver) blocked by Month (May, July, and August; 2-way ANOVAs).

a. Analysis of Variance for total no. epibenthic predators (fish + crabs)

| Source | DF | Seq SS | Adj SS | Adj MS | F | P |
|---|---|---|---|---|---|---|
| River | 1 | 8243 | 8243 | 8243 | 0.36 | 0.549 |
| Zone | 1 | 282594 | 282594 | 282594 | 12.51 | 0.001 |
| River*Zone | 1 | 30351 | 30351 | 30351 | 1.34 | 0.253 |
| Month | 2 | 614569 | 614569 | 307285 | 13.60 | 0.000 |
| Error | 42 | 948845 | 948845 | 22592 | | |
| Total | 47 | 1884601 | | | | |

b. Analysis of Variance for total number of fish

| Source | DF | Seq SS | Adj SS | Adj MS | F | P |
|---|---|---|---|---|---|---|
| River | 1 | 2080 | 2080 | 2080 | 0.10 | 0.750 |
| Zone | 1 | 225776 | 225776 | 225776 | 11.12 | 0.002 |
| River*Zone | 1 | 14770 | 14770 | 14770 | 0.73 | 0.399 |
| Month | 2 | 561232 | 561232 | 280616 | 13.82 | 0.000 |
| Error | 42 | 852711 | 852711 | 20303 | | |
| Total | 47 | 1656570 | | | | |

c. Analysis of Variance for Number of crabs

| Source | DF | Seq SS | Adj SS | Adj MS | F | P |
|---|---|---|---|---|---|---|
| River | 1 | 2041.0 | 2041.0 | 2041.0 | 8.33 | 0.006 |
| Zone | 1 | 3185.0 | 3185.0 | 3185.0 | 13.01 | 0.001 |
| River*Zone | 1 | 2775.5 | 2775.5 | 2775.5 | 11.33 | 0.002 |
| Month. | 2 | 1280.3 | 1280.3 | 640.1 | 2.61 | 0.085 |
| Error | 42 | 10285.6 | 10285.6 | 244.9 | | |
| Total | 47 | 19567.5 | | | | |

d. Analysis of Variance for York River number of crabs

| Source | DF | Seq SS | Adj SS | Adj MS | F | P |
|---|---|---|---|---|---|---|
| Zone | 1 | 5953.5 | 5953.5 | 5953.5 | 13.15 | 0.002 |
| Month | 2 | 1768.1 | 1768.1 | 884.0 | 1.95 | 0.168 |
| Error | 20 | 9052.3 | 9052.3 | 452.6 | | |
| Total | 23 | 16773.8 | | | | |

e. Analysis of Variance for Rappahannock River number of crabs

| Source | DF | Seq SS | Adj SS | Adj MS | F | P |
|---|---|---|---|---|---|---|
| Zone | 1 | 7.04 | 7.04 | 7.04 | 0.22 | 0.642 |
| Month | 2 | 114.25 | 114.25 | 57.12 | 1.81 | 0.190 |
| Error | 20 | 631.33 | 631.33 | 31.57 | | |
| Total | 23 | 752.62 | | | | |

Table 2.12 (Cont'd)
f. Analysis of Variance for Number of Spot across both rivers

| Source | DF | Seq SS | Adj SS | Adj MS | F | P |
|---|---|---|---|---|---|---|
| River | 1 | 6464 | 6464 | 6464 | 0.86 | 0.359 |
| Zone | 1 | 20460 | 20460 | 20460 | 2.72 | 0.106 |
| River*Zone | 1 | 46 | 46 | 46 | 0.01 | 0.938 |
| Month | 2 | 248917 | 248917 | 124458 | 16.55 | 0.000 |
| Error | 42 | 315753 | 315753 | 7518 | | |
| Total | 47 | 591640 | | | | |

g. Analysis of Variance for Number of Hogchoker across both rivers

| Source | DF | Seq SS | Adj SS | Adj MS | F | P |
|---|---|---|---|---|---|---|
| River | 1 | 27361 | 27361 | 27361 | 26.01 | 0.000 |
| Zone | 1 | 17557 | 17557 | 17557 | 16.69 | 0.000 |
| River*Zone | 1 | 24390 | 24390 | 24390 | 23.18 | 0.000 |
| Month. | 2 | 1973 | 1973 | 986 | 0.94 | 0.400 |
| Error | 42 | 44189 | 44189 | 1052 | | |
| Total | 47 | 115469 | | | | |

h. Analysis of Variance for York River number of hogchoker

| Source | DF | Seq SS | Adj SS | Adj MS | F | P |
|---|---|---|---|---|---|---|

| Source | DF | Seq SS | Adj SS | Adj MS | F | P |
|---|---|---|---|---|---|---|
| YkHi/lo | 1 | 41667 | 41667 | 41667 | 21.04 | 0.000 |
| YkMo | 2 | 4849 | 4849 | 2424 | 1.22 | 0.315 |
| Error | 20 | 39608 | 39608 | 1980 | | |
| Total | 23 | 86124 | | | | |

i. Analysis of Variance for Rappahannock River number of hogchoker

| Source | DF | Seq SS | Adj SS | Adj MS | F | P |
|---|---|---|---|---|---|---|

| Source | DF | Seq SS | Adj SS | Adj MS | F | P |
|---|---|---|---|---|---|---|
| RpHi/Lo | 1 | 280.17 | 280.17 | 280.17 | 3.55 | 0.074 |
| RapMonth | 2 | 127.75 | 127.75 | 63.87 | 0.81 | 0.459 |
| Error | 20 | 1576.58 | 1576.58 | 78.83 | | |
| Total | 23 | 1984.50 | | | | |

predators between the two river zones suggests that the effect of predation should also differ by river zone.

Predators in the York and Rappahannock Rivers showed similar patterns of size, and growth was apparent throughout the summer. For brevity, only the July York River size-frequencies are shown as representative of major patterns for both rivers in all sampling months. Many of the individuals collected in these shallow-water trawls were too small to feed effectively on macrofauna. For example, spot < 50 mm TL do not feed on macrofauna (Weinstein 1983).

Crabs showed a bimodal size-frequency distribution for both rivers in all three sampling months, both downriver (though few crabs were caught) and upriver, as evidenced in the York River in July (Fig. 2.13). In July, modes were apparent at 65 mm CW and 115 mm CW (Fig. 2.13).

Likewise, hogchoker in the York River (Fig. 2.14) showed bimodal size-frequency distribution upriver. In July, two modes were apparent upriver, one at 50 mm and one at 85 mm TL. Downriver few individuals were caught, though there was a single larger mode in size-frequency at 78 mm. In the Rappahannock, few hogchoker were present except in August in high salinity.

Spot were the most abundant predator throughout the summer (e.g., more than 80 individuals were collected upriver in the York in May) and showed no difference in size between river zones or rivers, though slightly larger fish were collected upriver in the York in July (Fig. 2.15). The size-distribution typically showed a unimodal peak that progressed from a mode of 30 (May) to 75 (July) to 106 mm TL (August) through the

Fig. 2.13. Population size structure of York River blue crabs (*Callinectes sapidus*) from 4 pooled trawls collected at Downriver and Upriver zones in July, 1994. Size class is measured in millimeters carapace width.

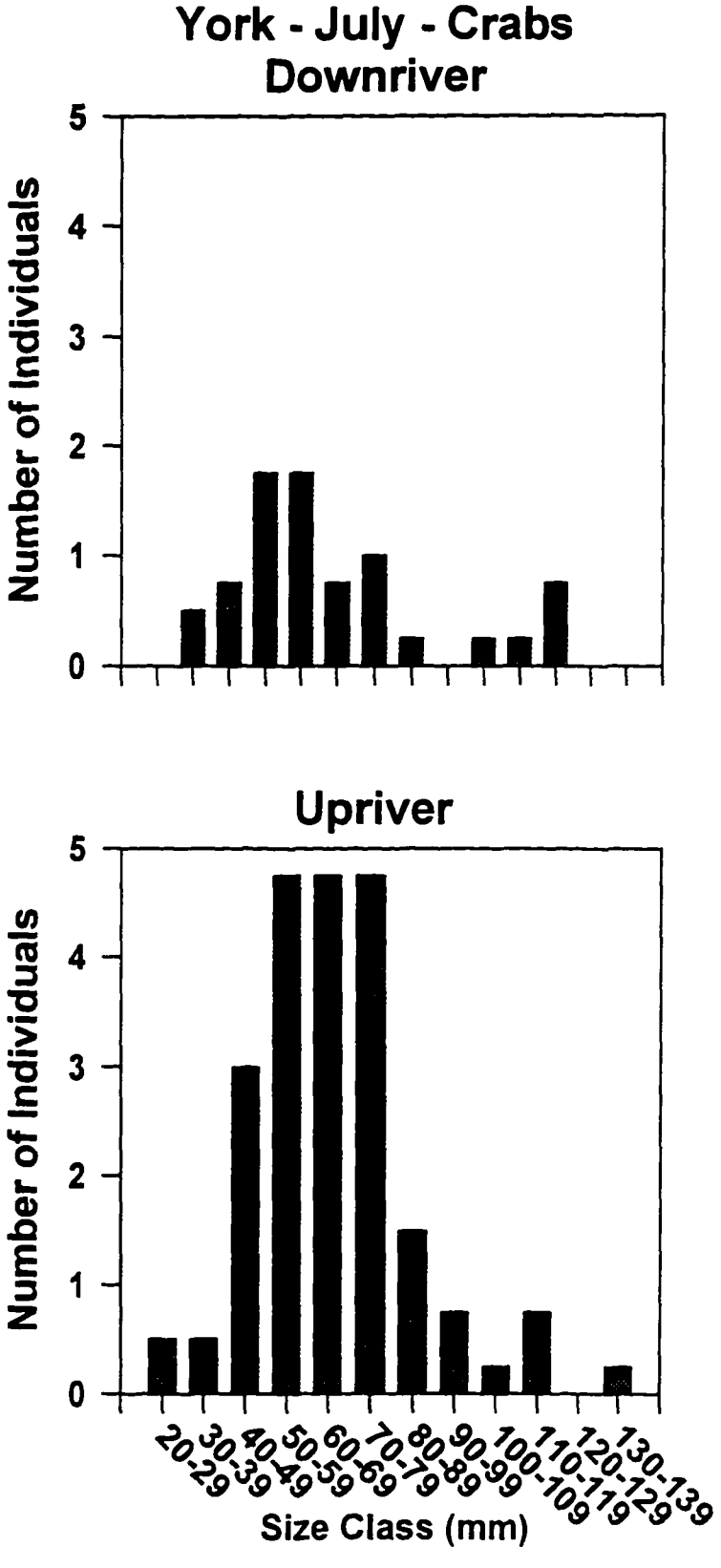


Fig. 2.14. Population size structure of York River hogchoker (*Trinectes maculatus*) from 4 pooled trawls collected at Downriver and Upriver zones in July, 1994. Size class is measured in millimeters total length.

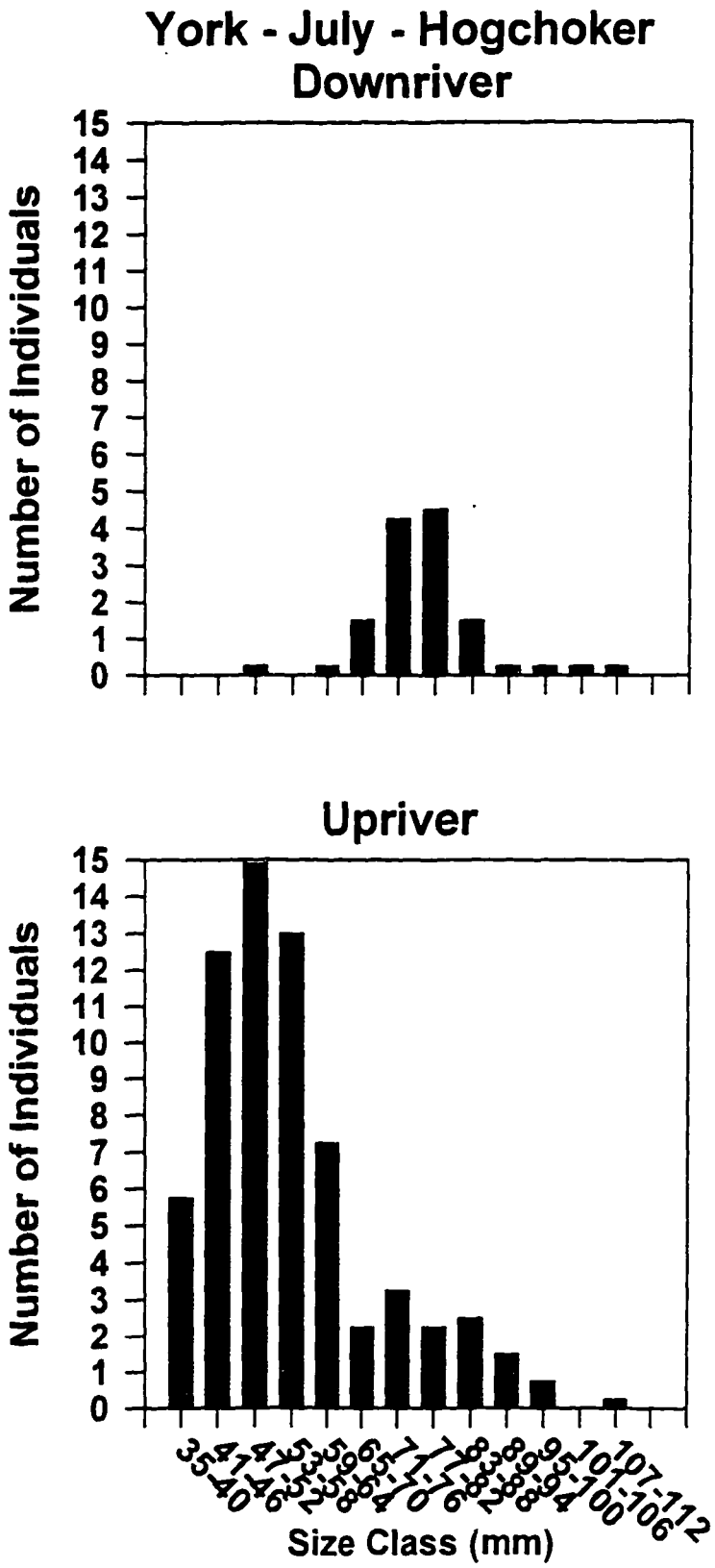
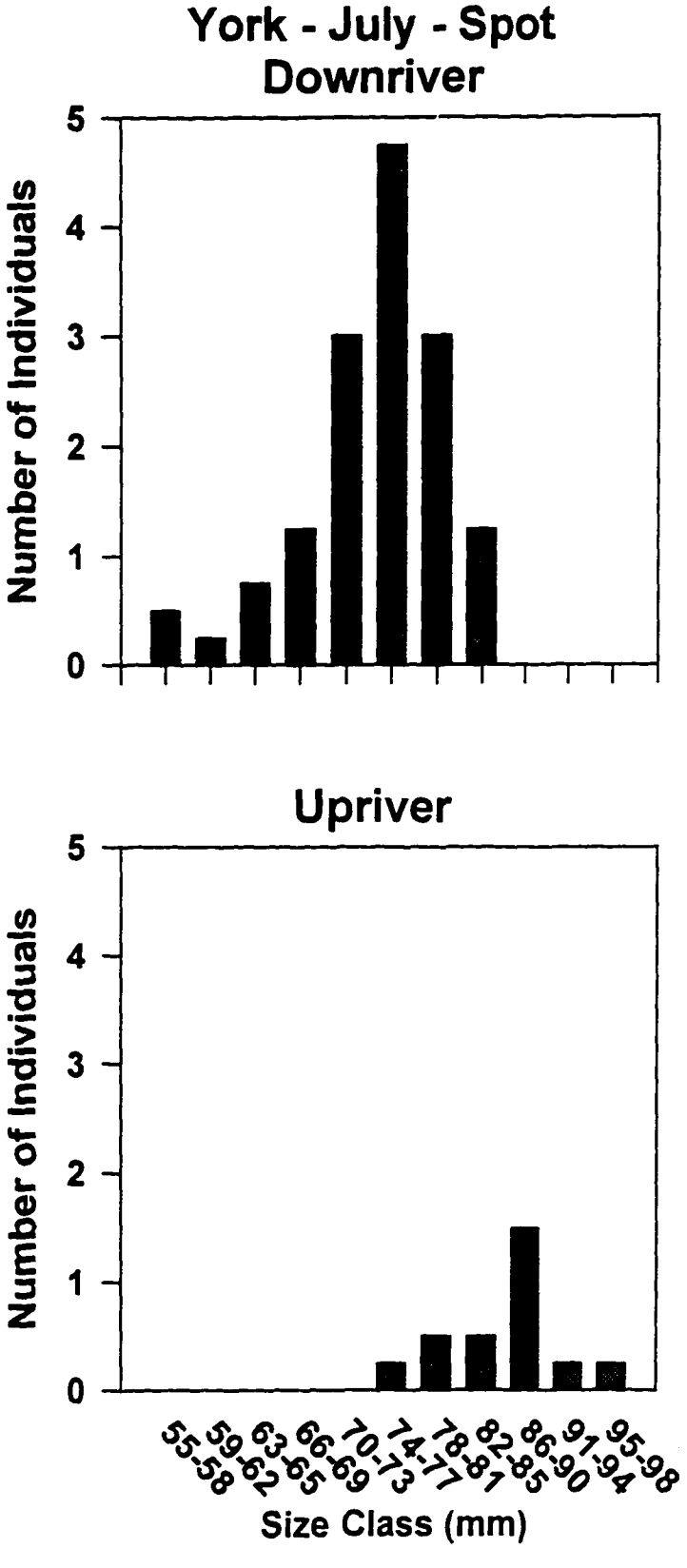


Fig. 2.15. Population size structure of York River spot (*Leiostomus xanthurus*) from 4 pooled trawls collected at Downriver and Upriver zones in July, 1994. Size class is measured in millimeters total length.



sampling months in the York (Fig 2.15). In the Rappahannock, a single cohort of spot grew from 23 to 74 to 101 mm TL from May to August downriver.

In summary, predators were most abundant upriver throughout the summer across both rivers. Blue crabs showed the greatest difference between zones (i.e., were much more abundant upriver) and thus their effect should be greatest upriver. Hogchoker were abundant only in the York, whereas spot were equally abundant in both rivers in both zones.

Finally, the effect of predation on benthic community structure can be determined by assessing the effect of predator removal or enhancement on consequent changes in species richness, evenness, or diversity (H' and Simpson's diversity) within the two zones. Laboratory evidence for predator activity around cages showed an increase in the 'roof only' and 'cage control' treatments. These treatments showed significantly higher diversity (both H' and $1-\lambda$) 12 weeks after deployment. Highest overall diversity in the natural community was found downriver, but upriver, in treatments where predators were enhanced, diversity increased.

## *DISCUSSION*

In this investigation, epibenthic predator abundance, prey abundance and the differential effect of predation along an estuarine gradient in the York River were quantified. The findings from this study are novel in suggesting that predation is more important to benthic diversity in an area of increased environmental stress (i.e., upriver). The major findings include that (1) diversity was lower upriver, (2) predator abundance was greater upriver, and (3) predator removal or enhancement had significant effects upriver and not downriver. The decreased diversity upriver was consistent with predictions from the MS model, however results of predator abundance and infaunal effects are not compatible with the model and therefore the MS model needs to be modified substantially to be implemented in this system. Higher stress upriver did not inhibit predators from entering that zone, nor from consuming infauna. Rather, predators appear to be drawn to upriver zones by the availability of food or preferable habitat (Weinstein 1983). Therefore, this benthic system appears to be driven by a combination of three things (1) salinity tolerance of prey organisms, (2) primary production and its ramifications for higher trophic levels and (3) predation. Bottom-up as well as top-down forces are important in controlling species diversity in this soft-bottom system.

**I. Infaunal abundance**

In this study, differences in infaunal abundance between sites were so great that they overshadowed most effects of predation at the species level. Downriver, the variability in abundance between sites was great, even without any cage treatment (Fig. 2.4). One site had much higher abundance than the others, and at this site, differences in predation (i.e., caging treatment) affected the abundances of infauna (e.g., for *Mercenaria mercenaria*).

For the abundant bivalve, *Mercenaria mercenaria*, the density within cages ('roof only') was significantly higher than that in areas exposed to predators ('cage control' and 'no cage') for one site. For *M. mercenaria*, when abundance was high, a significant cage treatment effect was detectable. At all other sites where abundance was low, no cage effect was detected. This suggests that in areas of low environmental stress (e.g., downriver), the effect of predation was increased with increased abundance or recruitment. This agrees with previous caging studies throughout Chesapeake Bay that have detected effects of predation at relatively high salinities when only one site was used (e.g., Virnstein 1979, Holland et al. 1980, Hines et al. 1990). These studies were also conducted earlier in the year when infauna is still recruiting and abundances may be higher. This implies that the MS model requires a slight modification to incorporate an increase in the importance of predation with elevated recruitment. Predation is only important at high infaunal abundances, otherwise, the system seems to be driven by recruitment limitation. This is corroborated in the experimental manipulations where downriver areas experience less severe changes in abundance and also show little effect of predator exclusion.

Therefore, much can be gained by looking closely at one species (See Chapter 3) or at a single site (e.g., Virnstein 1979).

Recruitment has been recognized as an important force structuring communities (Holland et al. 1985, Gaines and Roughgarden 1985, Roughgarden et al. 1985), and spawned a series of hypotheses based on the idea of supply-side ecology (Underwood and Fairweather 1989). Increased recruitment in some species leads to decreased evenness and thus decreased diversity if predators do not consume the new recruits. Thus, predation is more important at high recruitment levels, requiring an increased slope of the predation importance line along the axis of recruitment in the MS model (see Menge and Sutherland 1987). Predators aggregate in areas of high prey densities (Mansour and Lipcius 1991) and thus must have the greatest effects in areas of higher prey densities.

**II. Benthic species diversity**

Diversity typically declines from the mouth of the estuary towards the freshwater reaches (Boesch 1977). Accordingly, the natural community in the York River was composed of a richer and more diverse assemblage downriver. There were clearly two different species assemblages, one upriver, with few species, and one downriver with greater diversity. This shift in diversity of the natural community from more diverse downriver to less diverse upriver is consistent with the MS consumer stress model (Menge and Sutherland 1987); in more stressful habitats (e.g., upriver) diversity decreases. This pattern is similar to that found in estuaries world-wide (Remane and Schlieper 1971) and to that described for deeper areas along the axis of the York River (Boesch 1977).

The downriver benthic community was similar to those described in previous studies in the area (i.e., Virnstein 1977, Holland et al. 1987). In another caging study, Virnstein (1977) used a study site that was further downriver and in a sandier, poorly sorted substrate, thus Virnstein's H' diversity values were only slightly higher (averaging between 2.7 and 2.9 bits/indiv.). A few species found in the York River community are strictly estuarine and don't penetrate into freshwater or marine water (see Boesch 1977). The question tested herein was whether or not this variation in diversity could be explained by differential importance of predation in structuring communities in the separate river zones. A major difference between this study and those conducted along a stress gradient in the rocky intertidal habitat (e.g., Paine 1966) is that the species assemblage changes appreciably across the gradient. The effects of predation on diversity are confounded with a change in diversity due to salinity. This difference, however, points out that the MS model may be best applied to local spatial scales, where species composition is similar, or areas of more extreme stress (Menge and Olson 1990).

Investigations on forces structuring benthic hard-bottom communities have resulted in the Menge and Sutherland consumer stress model (MS). This model predicts that the importance of predation should be reduced in habitats with higher stress and that diversity should decrease with increasing environmental stress. Some investigators feel that soft-bottom systems are sufficiently different from hard bottom systems and therefore require different paradigms and models of regulation (Wilson 1991). I, however, argue that models developed for hard-bottom systems can be useful heuristic tools that can be examined and modified as necessary for soft-bottom systems. Based on predictions from

the MS model, it was expected that predation would have a greater effect in the downriver higher stress areas in the York River, but conversely, the importance of predation was demonstrably greater upriver.

**III. Caging artifacts & effects**

Predator exclusion cages have been used extensively to study biological interactions in soft sediments (Hall et al. 1990). If effects of caging are detected, the possibility of cage-induced artifacts must be investigated. If not deployed properly, cages can be ineffective as predator exclosures and may serve as small artificial reefs (Virnstein 1978). The presence of an elevated physical structure can also alter the hydrodynamics of the area, causing scouring or increased sedimentation (Naqvi 1968, McCall 1977). Cages may additionally enhance or reduce larval settlement (Woodin 1974). Thus, prior planning is needed for an assessment of cage efficiency and to avoid cage artifacts. In the least, potential caging artifacts should be inspected.

Examination of cage artifacts and effects produced a surprising result for predator behavior around the cages. In the laboratory, the 'full cage' was effective at excluding predators, but surprisingly the 'sides only' excluded all predators too. Additionally, the highest activity was seen in the 'roof only' and 'cage control' treatments, rather than the natural sediment (i.e., the 'no cage') treatment. A cage in a structureless soft-sediment environment can attract the very predators is designed to exclude, similar to the structure provided by natural reefs (Virnstein 1978), as was demonstrated in laboratory predator activity experiments. Furthermore, at a site where caging treatments are 3 m apart, a

predator may be attracted by a 'cage control' structure and thereby removed from a natural sediment area (i.e., 'no cage' treatment).

Activity of predators in the field should be analogous to those in the laboratory, although the presence of juvenile crabs presents an additional problem. Crabs are difficult to keep out of cages; they can dig below the sediment to enter or can enter through the mesh as juveniles and molt to a size that affects resident infauna (Virnstein 1978). Some crabs were occasionally found within the full cages, but were immediately removed and holes repaired. Thus, the main effect of cages was to enhance predator density at the 'roof only' and 'cage control', to allow natural densities in the 'no cage', to reduce densities 'sides only', and to eliminate predators in the 'full cage' treatment. Blue crabs were the most active predator in the cages and therefore were presumed to have the greatest effect in the field. The activities recorded in the lab correspond well to treatment effects in the field and thus support the contention that predators caused the observed treatment effects, either by consumption of infauna or by sediment disturbance. Additionally, sediment analyses, carbon and nitrogen analyses showed no significant effects of cages on sedimentary characteristics and therefore no caging artifacts are prominent.

A serendipitous outcome of the sediment analysis, however, was that upriver sediments were significantly finer and included more organic nutrients. A major focus of this study was not classification of benthic nutrients, but the trend seen in benthic carbon samples agrees well with other more comprehensive studies. For example, in deeper waters in the York River, there was a trend of increasing volatile solids with distance from the mouth of the York River (Dauer et al. 1989). Thus, the increased organic carbon and

increased C:N ratio upriver may be indicative of a better food source upriver. Though the values measured in this study are low compared to other estuarine areas (Valiela 1984), if the difference is real, this suggests that upriver areas potentially have higher food availability. The community may therefore be controlled by food availability or "bottom-up" forces.

If the community is controlled by "bottom-up" forces, then predators would be expected to aggregate in areas with higher food (Oksanen et al. 1981). Although I did not document increased abundances of infauna upriver, increased biomass could yield more food for consumers. If organisms at each trophic level are food limited (Fretwell 1977, 1987), and not controlled by predation, the system would be regulated by "bottom-up" forces only. A more plausible explanation, and one that fits the system examined herein, is that the system is regulated by co-limitation by predators and resources (Power 1992). This means that primary production provides a template for communities, and predation acts on top of that (Arditi and Ginzburg 1989, Menge and Olson 1990). The relative importance of food limitation depends on the importance of predation. Prey populations, though reduced by predation, can increase with increasing resources (Arditi and Ginzburg 1989). In addition to examining cage artifacts, it was necessary to examine predator abundance around the deployed cages.

**IV. Natural predator abundance**

The predators collected in this study were similar to those caught in deeper waters (Horwitz 1987, Hines et al. 1990), including the blue crab, *Callinectes sapidus*, as well as

various demersal fishes including spot, *Leiostomus xanthurus*, croaker, *Micropogonias undulatus*, and hogchoker, *Trinectes maculatus*. Hogchoker are known as abundant, nocturnal feeders (Dovel et al. 1969) which typically feed on epifauna and infauna such as mysids, cumaceans and polychaetes (Hildebrand and Schroeder 1928). Spot are dominant in the lower York (Mansour 1992) and also feed on infauna (Hildebrand and Schroeder 1928, Stickney et al. 1975). Blue crabs are omnivorous (Baird and Ulanowicz 1989), and feeding efficiency varies significantly with prey availability, predator density and habitat complexity (Blundon and Kennedy 1982a, b, Arnold 1984, Lipcius and Hines 1986, West and Williams 1986, Hines et al. 1990, Eggleston 1990, Mansour and Lipcius 1991, Eggleston et al. 1992). The diet of blue crabs, however, consists mainly of bivalve molluscs, predominantly *Mya* and *Macoma*, and conspecifics, as well as polychaetes, other crabs and fish (Laughlin 1982, Alexander 1986, Hines et al. 1990, Mansour 1992, Ebersole and Kennedy 1995). Based on this ecology, the dominant predators were expected to affect infauna as long as predators were present in the system.

The predator guild in Chesapeake Bay and its tributaries typically shows temporal variability (Hines et al. 1987, Horwitz 1987), as was true for this shallow-water study. The numerically dominant species characteristically enter the deeper water in Chesapeake Bay tributaries in summer (Hines et al. 1987). Usually, when *Leiostomus* xanthurus is abundant, *Micropogonias undulatus* will be reduced in abundance. Thus, the dominants may undergo seasonal or annual fluctuations in dominance, although the major species remain the same. The sciaenids typically show a single year class, as found in this study, and blue crabs typically show a bimodal size-distribution (Mansour 1991), as found here.

Additionally, predator abundance and distribution is likely controlled by habitat availability, as well as food availability (Weinstein and O'Neil 1986); estuarine fish use marsh nurseries and remain resident there in the summer months The dominant species showed significant growth during the foraging period, and these species were presumably feeding on infauna within the system throughout the summer, as has been previously demonstrated in predators gut content analysis (Mansour 1992).

Some of the predators caught in the shallow-water trawls were too small to feed on macrofauna, however, many were large enough. Small *Leiostomus xanthurus* and *Micropogonias undulatus* switch to a macrofaunal diet at about 50 mm (Livingston 1980, Weinstein 1983, Weinstein and O'Neil 1986), *Trinectes maculatus* switches to a diet of macrofauna at 30 mm (A. Hines, *unpublished data*), and blue crabs feed on macrofauna at about 60 mm (Laughlin 1982). Given the mean predator sizes seen in the York River, predation pressure on infauna was greatest during the month of July when juvenile sizes approached those where macrofauna could be eaten. The effect of predation could be either by consumption of individuals or by sediment disturbance (Virnstein 1979). Predator digging can disturb the sediment and increase suspended materials that adversely affect suspension feeders (sensu Rhodes and Young 1970). Additional predators, such as wading birds, which are known to feed on *Macoma balthica*, could influence infauna, but other birds were not likely important in this study since experimental sites were never exposed at low tide (Jorde and Haramis 1995). Knowing that epibenthic predators were in the system and large enough to feed on infauna, their effects on benthic diversity could be assessed.

## V. Summary

Regulation of benthic community structure has been studied extensively in marine systems and predation has emerged as an important regulating factor controlling species composition in some soft-bottom communities (Hines et al 1990, Virnstein 1979, Peterson 1979b, Holland et al. 1980, Dayton 1984, Quammen 1994). Predation by epibenthic fish and crabs was important in structuring portions of the shallow water soft-bottom community studied along the axis of the York River.

Predation was more important in regulating the benthic community upriver, where predators were more abundant, as evidenced by increased diversity in cage treatments that attracted predators. This conclusion was based on the following major findings of this study: (1) all measures of benthic diversity were lower upriver, (2) abundance of predators was greater upriver throughout the summer, (3) the greatest effect of predator removal or enhancement was in upriver areas. The importance of predation has been seen in other sections of Chesapeake Bay both high salinity (Virnstein 1979, Holland et al. 1980, Orth et al. 1984) and low salinity (Hines et al. 1990). The higher stress upriver did not inhibit predators from entering that zone, nor did it prevent them from feeding efficiently. Based on these findings, this system does not fit well with the MS model of consumer stress and the model must be modified to for the York River benthos.

There are several alternative mechanisms whereby predation can enhance diversity. Though intense predation can reduce diversity (Sammarco et al. 1974), predators can increase diversity by feeding preferentially on competitive dominants, thus allowing competitively inferior species to survive (Paine 1966, 1969). In contrast, in the absence of

predation, the competitive dominant could exploit the resources and prevent survival of additional species. This has been shown experimentally in the rocky intertidal where starfish were removed from a rocky shore and mussels increased in abundance, outcompeting other species (Paine 1974). In this way, predation maintains diversity in some rocky intertidal systems.

Predators can also increase diversity by feeding on all species to a density low enough that competitive exclusion is not a problem (Roughgarden and Feldman 1975). In this case, evenness would increase, as all species are maintained at relatively low densities. In the soft-bottom system of the York River, the elevated diversity was a consequence of both evenness and richness increasing in caging treatments that attracted predators. This suggests that upriver in the York, predators are non-selectively feeding on all infauna, reducing overall abundance and allowing more rare species to survive. The increase in evenness occurs across all species, not just through a competitive dominant (*sensu* Paine 1966). When predation is high enough, more species survive and evenness increases. Thus upriver, where predators are abundant, predation acts to regulate the infaunal community by increasing evenness, not by reducing competition.

Abundance and diversity were enhanced using exclusion cages in many soft-bottom caging studies (e.g., Virnstein 1977, 1979), but such studies were conducted at single sites and cages deployed earlier in the summer, while recruitment is occurring. In the present study, significant differences were only found upriver 12 weeks after cage deployment. The treatments that attracted predators had higher diversity (both H' and $\lambda$) than the others due to an increase in evenness and slight (non-significant) increase in

richness. This further suggests that, as in rocky intertidal habitats, predation may maintain diversity. In previous rocky intertidal studies, predators fed on a competitively dominant species reducing interspecific competition, allowing other species to survive. In this study, however, no single competitive dominant was reduced, but rather predation eliminated new recruits, thus reducing the abundance, and increasing evenness.

Competition has been proven important in a number of soft-bottom systems (Woodin 1983). Although some studies show a significant effect of competition (Woodin 1974, Roe 1975, Peterson 1977, Peterson and Andre 1980, Levin 1981, Tamaki 1985), predation, recruitment processes, and environmental stress appear more important as structuring forces in soft-sediment communities (Dayton 1984, Wilson 1991). In this study, diversity was not increased through elimination of a competitive dominant, but rather by increasing evenness of all species.

The effect of predation was enhanced upriver in higher stress. Elevated predator abundance upriver in a higher stress zone may be a consequence of increased production of organics and associated infauna; predators aggregate where the prey are concentrated. Thus, predators are controlled by prey abundance, or "bottom-up" forces (Power 1992) and prey are controlled by predators, or "top-down" forces. This benthic system may therefore be driven by a combination of salinity tolerance, primary production and predation.

On a local scale (i.e., upriver), variation in predation pressure (i.e., enhanced predation in the 'roof only' and 'cage control' treatments) significantly affected diversity. Diversity was increased with elevated predator density, thus, predation maintained

diversity. On a broader scale (i.e., comparing upriver to downriver), differences in diversity could not be explained by predation. If predation was more important in downriver low stress areas compared to upriver high stress areas (as predicted by the MS model), then the 'full cage' treatment would have larger effects downriver than upriver. The low predator density downriver explains why this did not occur. Differences in diversity upriver versus downriver are driven by physical tolerances of infauna and not by predation, as is typical in estuaries worldwide (Remane and Schlieper 1971, Boesch 1977, Wolff 1983, Day et al. 1989).

To summarize, species diversity was lowest upriver, and predator abundance was enhanced upriver. Predators had greatest effects upriver. Laboratory evidence was consistent with benthic diversity evidence showing that predators were attracted to the 'roof only' and 'cage control' treatments where they increased diversity. The mechanism of increasing diversity was through reducing densities in abundant species, thus increasing evenness. The effect of predation was thereby increased with elevated recruitment, but the MS model predicts a decreasing importance of predation with increased recruitment. Thus, to apply the Menge and Sutherland model to this soft-bottom system, a modification for increased importance of predation at high recruitment levels is necessary.

Predation is important in regulating the benthic community at small local scales, thus a "top-down" model of community regulation is appropriate. Though predation acts to increase diversity upriver, predation alone is not enough to increase diversity to levels as high as those downriver. Physiological tolerances of estuarine species drive the larger-scale patterns in diversity. Additionally, organic nutrients were elevated upriver, where

predators concentrated. Predators were not deterred by higher stress in these low salinity areas with fluctuating physical conditions. Rather, they were concentrating where augmented food was available. This suggests that the system may not be governed solely by "top-down" forces (i.e., a consumer stress model), but that a production model incorporating "bottom-up" control of the benthos may also be appropriate (Menge and Olson 1990). This system is influenced by both production and predation and therefore requires a mix of "top-down" and "bottom-up" control as has been identified in other systems (Power 1992). In conclusion, predation is somewhat important in regulating the York River benthic community, but the community is potentially governed by co-limitation of "top-down" and "bottom-up" forces.

## APPENDIX I

Species list for species found in either river zone in the York. Most common species are listed by phyla, rare species are identified by letters indicating phyla: P = polychaete, I = isopod, A = amphipod, B = bivalve, O = oligochaete, Ph = phoronid, G = gastropod, Ar = arthropod.

**Polychaetes:**

1. *Arabellidae (Drilonereis longa)*
2. *Clymenella torquata*
3. *Glycinde solitaria*
4. *Gyptis vittata now Gyptis crypta*
5. *Heteromastus filiformis*
6. *Nereis succinea*
7. *Paraprionospio pinnata*
8. *Phyllodoce sp.*
9. *Scoloplos sp.*
10. *Spio sp.*
11. *Spiochaetopterus oculata*
12. *Spiophanes bombyx*
13. *Streblospio benedicti*
14. *Tharyx sp.*

**Molluscs:**

15. *Acteocina canaliculata*
16. *Macoma balthica*
17. *Macoma mitchelli*
18. *Mercenaria mercenaria*
19. *Mulinea lateralis*

**Crustaceans:**

20. *Caprellidae*
21. *Cyanthura polita*
22. *Gammarus sp.*
23. *Leucon americana*
24. *Listriella clymenellae*
25. *Mysidopsis bigelowi*
26. *Oxyurostylis smithi*

**Other:**

27. *Hemichordata*
28. *Lanceolet*
29. *Nemertina*
30. *Phoronida*
31. *Platyhelminthes*
32. *Tubificidae*

**(Appendix I Contd)**

**Rare Species:**

33. Solelepis *sp. (P)*
34. *Loimia medusa (P)*
35. *Chiridotea (I)*
36. *Ampelisca sp. (A)*
37. *Anadara transversa (G)*
38. *Anemone (Cnidarian)*
39. *Assinea succinea (G)*
40. *Callinectes sapidus (Ar, Crab)*
41. *Corophium (A)*
42. *Cyclapsis varians (Ar, Cumacean)*
43. *Edotea triloba (I)*
44. *Holothurian (Sea cucumber)*
45. *Mediomastus ambiseta (P)*
46. *Monoculoides edwardsi (Amph.)*
47. *Mya arenaria (M)*
48. *Ogyrides alphaetostis (I)*
49. *Pinnixa sp.(Ar, Crab)*
50. *Polydora ligni (P)*
51. *Sayella sp. (G)*
52. *Stenothoe minuta (A)*
53. *Tagelus plebius (M)*
54. *Xanthidae (Ar, Crab)*
55. *Acorn worms (Enteropneusts)*
56. *Chaetozone sp. (P-cirratulid)*
57. *Gemma gemma (M)*
58. *Glycera americana (P)*
59. *Isopoda #1 (I)*
60. *Macoma tenta (M)*
61. *Mitrella lunata (G)*
62. *Mysidopsis neomysis (Ar, shrimp)*
63. *Orbinidae (P)*
64. *Oxyorostylis smithi (Ar, Cumacean)*
65. *Pectinaria gouldi (P)*
66. *Polinices duplicatus (G)*
67. *Pseudurythoe paucibranchiata (P)*
68. *Rangia cuneata (M)*
69. *Retusa obtusa (M)*
70. *Teinostoma (G)*

**APPENDIX II.** Mean diversity measures for each site and each time period from 3 benthic subsamples. Measures include richness (no sp), abundance (indiv), Shannon-Wiener diversity (h-prime), Simpson's index (lambda), and evenness (even). For week 0, only 'no cage' treatement was sampled, means by site are given. Other time periods listed by cage type. Five caging treatments include 1 = full cage, 2 = roof only, 3 = sides only, 4 = cage control, and 5 = no cage. Time periods include 1 = week 0, 2 = week 6, 3 = week 12. Sites include YH (York high = downriver) and YL (York low = upriver).

**1YH**

| Variable | Site | N | Mean | Median | TrMean | StDev | SEMean |
|---|---|---|---|---|---|---|---|
| No.Spec | 1 | 3 | 9.00 | 11.00 | 9.00 | 3.46 | 2.00 |
| | 2 | 3 | 12.333 | 13.000 | 12.333 | 1.155 | 0.667 |
| | 3 | 3 | 6.67 | 6.00 | 6.67 | 2.08 | 1.20 |
| | 4 | 3 | 9.00 | 9.00 | 9.00 | 2.00 | 1.15 |
| No.Indiv | 1 | 3 | 17.00 | 15.00 | 17.00 | 6.24 | 3.61 |
| | 2 | 3 | 42.33 | 41.00 | 42.33 | 6.11 | 3.53 |
| | 3 | 3 | 12.67 | 8.00 | 12.67 | 8.08 | 4.67 |
| | 4 | 3 | 19.00 | 19.00 | 19.00 | 2.00 | 1.15 |
| H-prime | 1 | 3 | 2.707 | 3.100 | 2.707 | 0.806 | 0.465 |
| | 2 | 3 | 3.0600 | 3.0200 | 3.0600 | 0.1637 | 0.0945 |
| | 3 | 3 | 2.490 | 2.410 | 2.490 | 0.376 | 0.217 |
| | 4 | 3 | 2.600 | 2.390 | 2.600 | 0.381 | 0.220 |
| Lambda | 1 | 3 | 0.2233 | 0.1500 | 0.2233 | 0.1447 | 0.0835 |
| | 2 | 3 | 0.15667 | 0.16000 | 0.15667 | 0.01528 | 0.00882 |
| | 3 | 3 | 0.2100 | 0.2200 | 0.2100 | 0.0458 | 0.0265 |
| | 4 | 3 | 0.2400 | 0.2400 | 0.2400 | 0.0700 | 0.0404 |
| Evenness | 1 | 3 | 0.8700 | 0.9000 | 0.8700 | 0.0889 | 0.0513 |
| | 2 | 3 | 0.8467 | 0.8400 | 0.8467 | 0.0306 | 0.0176 |
| | 3 | 3 | 0.92667 | 0.93000 | 0.92667 | 0.00577 | 0.00333 |
| | 4 | 3 | 0.8300 | 0.8500 | 0.8300 | 0.0624 | 0.0361 |

**1YL**

| | site | N | MEAN | MEDIAN | TRMEAN | STDEV | SEMEAN |
|---|---|---|---|---|---|---|---|
| no sp | 1 | 3 | 5.333 | 5.000 | 5.333 | 0.577 | 0.333 |
| | 2 | 3 | 6.00 | 5.00 | 6.00 | 2.65 | 1.53 |
| | 3 | 3 | 3.333 | 3.000 | 3.333 | 0.577 | 0.333 |
| | 4 | 3 | 6.33 | 7.00 | 6.33 | 2.08 | 1.20 |
| indiv | 1 | 3 | 8.67 | 10.00 | 8.67 | 3.21 | 1.86 |
| | 2 | 3 | 12.67 | 10.00 | 12.67 | 8.33 | 4.81 |
| | 3 | 3 | 10.00 | 11.00 | 10.00 | 2.65 | 1.53 |
| | 4 | 3 | 9.00 | 10.00 | 9.00 | 3.61 | 2.08 |
| h-prime | 1 | 3 | 2.253 | 2.320 | 2.253 | 0.266 | 0.154 |
| | 2 | 3 | 2.323 | 2.250 | 2.323 | 0.514 | 0.297 |
| | 3 | 3 | 1.3733 | 1.3800 | 1.3733 | 0.0503 | 0.0291 |
| | 4 | 3 | 2.430 | 2.450 | 2.430 | 0.500 | 0.289 |
| lambda | 1 | 3 | 0.2367 | 0.2000 | 0.2367 | 0.0723 | 0.0418 |
| | 2 | 3 | 0.2267 | 0.2200 | 0.2267 | 0.0702 | 0.0406 |
| | 3 | 3 | 0.4533 | 0.4400 | 0.4533 | 0.0321 | 0.0186 |
| | 4 | 3 | 0.2200 | 0.2400 | 0.2200 | 0.0721 | 0.0416 |
| even | 1 | 3 | 0.9333 | 0.9600 | 0.9333 | 0.0833 | 0.0481 |
| | 2 | 3 | 0.9300 | 0.9200 | 0.9300 | 0.0361 | 0.0208 |
| | 3 | 3 | 0.8033 | 0.8300 | 0.8033 | 0.0833 | 0.0481 |
| | 4 | 3 | 0.9333 | 0.9600 | 0.9333 | 0.0551 | 0.0318 |

**2YH1**

| Variable | treatmt | N | Mean | Median | TrMean | StDev | SEMean |
|---|---|---|---|---|---|---|---|
| sp | 1 | 3 | 13.67 | 13.00 | 13.67 | 2.08 | 1.20 |
| | 2 | 3 | 10.333 | 10.000 | 10.333 | 1.528 | 0.882 |
| | 3 | 3 | 15.000 | 15.000 | 15.000 | 0.000 | 0.000 |
| | 4 | 3 | 5.67 | 5.00 | 5.67 | 2.08 | 1.20 |
| | 5 | 3 | 14.333 | 14.000 | 14.333 | 0.577 | 0.333 |
| n | 1 | 3 | 36.67 | 43.00 | 36.67 | 13.65 | 7.88 |
| | 2 | 3 | 27.67 | 26.00 | 27.67 | 10.60 | 6.12 |
| | 3 | 3 | 49.67 | 59.00 | 49.67 | 17.04 | 9.84 |
| | 4 | 3 | 7.00 | 8.00 | 7.00 | 2.65 | 1.53 |
| | 5 | 3 | 27.67 | 28.00 | 27.67 | 7.51 | 4.33 |
| h prime | 1 | 3 | 3.363 | 3.460 | 3.363 | 0.374 | 0.216 |
| | 2 | 3 | 3.097 | 3.050 | 3.097 | 0.234 | 0.135 |
| | 3 | 3 | 2.997 | 3.050 | 2.997 | 0.492 | 0.284 |
| | 4 | 3 | 2.370 | 2.160 | 2.370 | 0.509 | 0.294 |
| | 5 | 3 | 3.490 | 3.490 | 3.490 | 0.230 | 0.133 |
| lambda | 1 | 3 | 0.1233 | 0.1000 | 0.1233 | 0.0493 | 0.0285 |
| | 2 | 3 | 0.1400 | 0.1500 | 0.1400 | 0.0265 | 0.0153 |
| | 3 | 3 | 0.2167 | 0.1800 | 0.2167 | 0.1097 | 0.0633 |
| | 4 | 3 | 0.2133 | 0.2500 | 0.2133 | 0.0635 | 0.0367 |
| | 5 | 3 | 0.1133 | 0.1200 | 0.1133 | 0.0306 | 0.0176 |
| e | 1 | 3 | 0.8967 | 0.9200 | 0.8967 | 0.0874 | 0.0504 |
| | 2 | 3 | 0.92000 | 0.92000 | 0.92000 | 0.01000 | 0.00577 |
| | 3 | 3 | 0.7667 | 0.7800 | 0.7667 | 0.1305 | 0.0754 |
| | 4 | 3 | 0.9700 | 0.9800 | 0.9700 | 0.0361 | 0.0208 |
| | 5 | 3 | 0.9100 | 0.8900 | 0.9100 | 0.0624 | 0.0361 |

**2YH2**

| Variable | treatmt | N | Mean | Median | TrMean | StDev | SEMean |
|---|---|---|---|---|---|---|---|
| sp | 1 | 3 | 10.667 | 11.000 | 10.667 | 0.577 | 0.333 |
| | 2 | 3 | 9.00 | 9.00 | 9.00 | 3.00 | 1.73 |
| | 3 | 3 | 11.33 | 12.00 | 11.33 | 2.08 | 1.20 |
| | 4 | 3 | 10.33 | 9.00 | 10.33 | 2.31 | 1.33 |
| | 5 | 3 | 8.00 | 10.00 | 8.00 | 3.46 | 2.00 |
| n | 1 | 3 | 53.0 | 40.0 | 53.0 | 26.1 | 15.0 |
| | 2 | 3 | 48.3 | 53.0 | 48.3 | 34.2 | 19.8 |
| | 3 | 3 | 59.00 | 56.00 | 59.00 | 13.75 | 7.94 |
| | 4 | 3 | 33.67 | 29.00 | 33.67 | 8.96 | 5.17 |
| | 5 | 3 | 30.3 | 34.0 | 30.3 | 17.8 | 10.3 |
| h prime | 1 | 3 | 2.663 | 2.830 | 2.663 | 0.463 | 0.267 |
| | 2 | 3 | 1.917 | 1.680 | 1.917 | 0.436 | 0.252 |
| | 3 | 3 | 2.910 | 2.830 | 2.910 | 0.259 | 0.150 |
| | 4 | 3 | 2.870 | 2.720 | 2.870 | 0.269 | 0.155 |
| | 5 | 3 | 2.620 | 2.980 | 2.620 | 0.694 | 0.401 |
| lambda | 1 | 3 | 0.2467 | 0.1900 | 0.2467 | 0.1343 | 0.0775 |
| | 2 | 3 | 0.423 | 0.530 | 0.423 | 0.185 | 0.107 |
| | 3 | 3 | 0.1733 | 0.1700 | 0.1733 | 0.0451 | 0.0260 |
| | 4 | 3 | 0.1867 | 0.1900 | 0.1867 | 0.0252 | 0.0145 |
| | 5 | 3 | 0.2000 | 0.1500 | 0.2000 | 0.0954 | 0.0551 |
| e | 1 | 3 | 0.7833 | 0.8200 | 0.7833 | 0.1484 | 0.0857 |
| | 2 | 3 | 0.643 | 0.520 | 0.643 | 0.258 | 0.149 |
| | 3 | 3 | 0.8367 | 0.8700 | 0.8367 | 0.0757 | 0.0437 |
| | 4 | 3 | 0.85667 | 0.86000 | 0.85667 | 0.00577 | 0.00333 |
| | 5 | 3 | 0.91000 | 0.91000 | 0.91000 | 0.01000 | 0.00577 |

**2YH3**

| Variable | treatmt | N | Mean | Median | TrMean | StDev | SEMean |
|---|---|---|---|---|---|---|---|
| sp | 1 | 3 | 6.333 | 7.000 | 6.333 | 1.155 | 0.667 |
| | 2 | 3 | 8.67 | 11.00 | 8.67 | 4.04 | 2.33 |
| | 3 | 3 | 11.00 | 9.00 | 11.00 | 3.46 | 2.00 |
| | 4 | 3 | 9.00 | 8.00 | 9.00 | 1.73 | 1.00 |
| | 5 | 3 | 10.00 | 9.00 | 10.00 | 2.65 | 1.53 |
| n | 1 | 3 | 14.00 | 13.00 | 14.00 | 6.56 | 3.79 |
| | 2 | 3 | 18.33 | 23.00 | 18.33 | 10.79 | 6.23 |
| | 3 | 3 | 22.67 | 17.00 | 22.67 | 9.81 | 5.67 |
| | 4 | 3 | 20.67 | 22.00 | 20.67 | 5.13 | 2.96 |
| | 5 | 3 | 27.00 | 25.00 | 27.00 | 8.19 | 4.73 |
| h prime | 1 | 3 | 2.393 | 2.400 | 2.393 | 0.230 | 0.133 |
| | 2 | 3 | 2.720 | 3.130 | 2.720 | 0.807 | 0.466 |
| | 3 | 3 | 3.063 | 2.820 | 3.063 | 0.421 | 0.243 |
| | 4 | 3 | 3.040 | 2.940 | 3.040 | 0.312 | 0.180 |
| | 5 | 3 | 2.767 | 2.680 | 2.767 | 0.214 | 0.123 |
| lambda | 1 | 3 | 0.2200 | 0.2300 | 0.2200 | 0.0361 | 0.0208 |
| | 2 | 3 | 0.1967 | 0.1400 | 0.1967 | 0.1159 | 0.0669 |
| | 3 | 3 | 0.1567 | 0.1800 | 0.1567 | 0.0404 | 0.0233 |
| | 4 | 3 | 0.1333 | 0.1400 | 0.1333 | 0.0306 | 0.0176 |
| | 5 | 3 | 0.2100 | 0.2200 | 0.2100 | 0.0173 | 0.0100 |
| e | 1 | 3 | 0.9033 | 0.9300 | 0.9033 | 0.0462 | 0.0267 |
| | 2 | 3 | 0.9167 | 0.9100 | 0.9167 | 0.0208 | 0.0120 |
| | 3 | 3 | 0.89667 | 0.89000 | 0.89667 | 0.01155 | 0.00667 |
| | 4 | 3 | 0.9633 | 0.9800 | 0.9633 | 0.0289 | 0.0167 |
| | 5 | 3 | 0.8433 | 0.8500 | 0.8433 | 0.0306 | 0.0176 |

**2YH4**

| Variable | treatmt | N | Mean | Median | TrMean | StDev | SEMean |
|---|---|---|---|---|---|---|---|
| sp | 1 | 3 | 9.00 | 9.00 | 9.00 | 3.00 | 1.73 |
| | 2 | 3 | 9.667 | 10.000 | 9.667 | 0.577 | 0.333 |
| | 3 | 3 | 9.00 | 8.00 | 9.00 | 1.73 | 1.00 |
| | 4 | 3 | 9.667 | 10.000 | 9.667 | 0.577 | 0.333 |
| | 5 | 3 | 12.000 | 12.000 | 12.000 | 1.000 | 0.577 |
| n | 1 | 3 | 19.33 | 17.00 | 19.33 | 10.69 | 6.17 |
| | 2 | 3 | 20.00 | 19.00 | 20.00 | 4.58 | 2.65 |
| | 3 | 3 | 20.33 | 16.00 | 20.33 | 9.29 | 5.36 |
| | 4 | 3 | 20.00 | 18.00 | 20.00 | 4.36 | 2.52 |
| | 5 | 3 | 21.67 | 20.00 | 21.67 | 4.73 | 2.73 |
| h prime | 1 | 3 | 3.013 | 3.120 | 3.013 | 0.459 | 0.265 |
| | 2 | 3 | 3.1100 | 3.0800 | 3.1100 | 0.0608 | 0.0351 |
| | 3 | 3 | 2.850 | 2.840 | 2.850 | 0.175 | 0.101 |
| | 4 | 3 | 2.973 | 2.890 | 2.973 | 0.180 | 0.104 |
| | 5 | 3 | 3.2867 | 3.3100 | 3.2867 | 0.0777 | 0.0448 |
| lambda | 1 | 3 | 0.1333 | 0.1200 | 0.1333 | 0.0416 | 0.0240 |
| | 2 | 3 | 0.13000 | 0.13000 | 0.13000 | 0.01000 | 0.00577 |
| | 3 | 3 | 0.1667 | 0.1600 | 0.1667 | 0.0208 | 0.0120 |
| | 4 | 3 | 0.1533 | 0.1600 | 0.1533 | 0.0306 | 0.0176 |
| | 5 | 3 | 0.12667 | 0.13000 | 0.12667 | 0.00577 | 0.00333 |
| e | 1 | 3 | 0.96667 | 0.97000 | 0.96667 | 0.01528 | 0.00882 |
| | 2 | 3 | 0.9533 | 0.9600 | 0.9533 | 0.0208 | 0.0120 |
| | 3 | 3 | 0.9067 | 0.8900 | 0.9067 | 0.0379 | 0.0219 |
| | 4 | 3 | 0.9100 | 0.9100 | 0.9100 | 0.0500 | 0.0289 |
| | 5 | 3 | 0.9167 | 0.9300 | 0.9167 | 0.0231 | 0.0133 |

**2YL1**

| Variable | trt | N | Mean | Median | TrMean | StDev | SEMean |
|---|---|---|---|---|---|---|---|
| no sp | 1 | 3 | 5.000 | 5.000 | 5.000 | 1.000 | 0.577 |
| | 2 | 3 | 9.00 | 8.00 | 9.00 | 1.73 | 1.00 |
| | 3 | 3 | 5.67 | 5.00 | 5.67 | 3.06 | 1.76 |
| | 4 | 3 | 7.00 | 8.00 | 7.00 | 1.73 | 1.00 |
| | 5 | 3 | 4.333 | 5.000 | 4.333 | 1.155 | 0.667 |
| indiv | 1 | 3 | 18.33 | 21.00 | 18.33 | 11.24 | 6.49 |
| | 2 | 3 | 33.33 | 38.00 | 33.33 | 13.61 | 7.86 |
| | 3 | 3 | 13.33 | 12.00 | 13.33 | 11.06 | 6.39 |
| | 4 | 3 | 26.67 | 29.00 | 26.67 | 10.69 | 6.17 |
| | 5 | 3 | 9.67 | 9.00 | 9.67 | 5.03 | 2.91 |
| hpr | 1 | 3 | 2.0967 | 2.1300 | 2.0967 | 0.1626 | 0.0939 |
| | 2 | 3 | 2.793 | 2.710 | 2.793 | 0.333 | 0.192 |
| | 3 | 3 | 2.173 | 2.120 | 2.173 | 0.622 | 0.359 |
| | 4 | 3 | 2.3433 | 2.3100 | 2.3433 | 0.0757 | 0.0437 |
| | 5 | 3 | 1.973 | 2.110 | 1.973 | 0.403 | 0.233 |
| lambda | 1 | 3 | 0.2600 | 0.2800 | 0.2600 | 0.0346 | 0.0200 |
| | 2 | 3 | 0.1767 | 0.1800 | 0.1767 | 0.0451 | 0.0260 |
| | 3 | 3 | 0.2533 | 0.2600 | 0.2533 | 0.0802 | 0.0463 |
| | 4 | 3 | 0.2533 | 0.2600 | 0.2533 | 0.0404 | 0.0233 |
| | 5 | 3 | 0.2767 | 0.2600 | 0.2767 | 0.0764 | 0.0441 |
| even | 1 | 3 | 0.9167 | 0.9600 | 0.9167 | 0.0839 | 0.0484 |
| | 2 | 3 | 0.8833 | 0.9000 | 0.8833 | 0.0379 | 0.0219 |
| | 3 | 3 | 0.9333 | 0.9100 | 0.9333 | 0.0586 | 0.0338 |
| | 4 | 3 | 0.8567 | 0.8100 | 0.8567 | 0.1172 | 0.0677 |
| | 5 | 3 | 0.9533 | 0.9600 | 0.9533 | 0.0404 | 0.0233 |

**2YL2**

| Variable | trt | N | Mean | Median | TrMean | StDev | SEMean |
|---|---|---|---|---|---|---|---|
| no sp | 1 | 3 | 6.333 | 6.000 | 6.333 | 0.577 | 0.333 |
| | 2 | 3 | 6.000 | 6.000 | 6.000 | 1.000 | 0.577 |
| | 3 | 3 | 6.333 | 6.000 | 6.333 | 0.577 | 0.333 |
| | 4 | 3 | 5.33 | 7.00 | 5.33 | 4.73 | 2.73 |
| | 5 | 3 | 7.333 | 7.000 | 7.333 | 1.528 | 0.882 |
| indiv | 1 | 3 | 51.0 | 31.0 | 51.0 | 38.2 | 22.0 |
| | 2 | 3 | 25.67 | 20.00 | 25.67 | 10.69 | 6.17 |
| | 3 | 3 | 49.33 | 52.00 | 49.33 | 4.62 | 2.67 |
| | 4 | 3 | 22.7 | 31.0 | 22.7 | 19.9 | 11.5 |
| | 5 | 3 | 29.00 | 28.00 | 29.00 | 8.54 | 4.93 |
| hpr | 1 | 3 | 2.1267 | 2.1700 | 2.1267 | 0.1498 | 0.0865 |
| | 2 | 3 | 2.3167 | 2.3200 | 2.3167 | 0.1650 | 0.0953 |
| | 3 | 3 | 2.3633 | 2.4500 | 2.3633 | 0.1501 | 0.0867 |
| | 4 | 3 | 1.547 | 2.020 | 1.547 | 1.373 | 0.792 |
| | 5 | 3 | 2.407 | 2.320 | 2.407 | 0.290 | 0.167 |
| lambda | 1 | 3 | 0.2900 | 0.3100 | 0.2900 | 0.0436 | 0.0252 |
| | 2 | 3 | 0.2233 | 0.2300 | 0.2233 | 0.0208 | 0.0120 |
| | 3 | 3 | 0.2233 | 0.2300 | 0.2233 | 0.0208 | 0.0120 |
| | 4 | 3 | 0.1833 | 0.2100 | 0.1833 | 0.1716 | 0.0991 |
| | 5 | 3 | 0.2333 | 0.2500 | 0.2333 | 0.0379 | 0.0219 |
| even | 1 | 3 | 0.8000 | 0.7700 | 0.8000 | 0.0608 | 0.0351 |
| | 2 | 3 | 0.9033 | 0.9000 | 0.9033 | 0.0252 | 0.0145 |
| | 3 | 3 | 0.8900 | 0.8700 | 0.8900 | 0.0529 | 0.0306 |
| | 4 | 3 | 0.517 | 0.720 | 0.517 | 0.451 | 0.260 |
| | 5 | 3 | 0.84333 | 0.84000 | 0.84333 | 0.01528 | 0.00882 |

**2YL3**

| Variable | trt | N | Mean | Median | TrMean | StDev | SEMean |
|---|---|---|---|---|---|---|---|
| no sp | 1 | 3 | 7.333 | 7.000 | 7.333 | 0.577 | 0.333 |
| | 2 | 3 | 7.0000 | 7.0000 | 7.0000 | 0.0000 | 0.0000 |
| | 3 | 3 | 8.000 | 8.000 | 8.000 | 1.000 | 0.577 |
| | 4 | 3 | 6.667 | 6.000 | 6.667 | 1.155 | 0.667 |
| | 5 | 3 | 7.000 | 7.000 | 7.000 | 1.000 | 0.577 |
| indiv | 1 | 3 | 31.67 | 36.00 | 31.67 | 7.51 | 4.33 |
| | 2 | 3 | 40.33 | 39.00 | 40.33 | 8.08 | 4.67 |
| | 3 | 3 | 39.67 | 42.00 | 39.67 | 4.93 | 2.85 |
| | 4 | 3 | 38.7 | 33.0 | 38.7 | 18.2 | 10.5 |
| | 5 | 3 | 34.00 | 40.00 | 34.00 | 10.39 | 6.00 |
| hpr | 1 | 3 | 2.383 | 2.430 | 2.383 | 0.313 | 0.180 |
| | 2 | 3 | 2.387 | 2.470 | 2.387 | 0.199 | 0.115 |
| | 3 | 3 | 2.340 | 2.440 | 2.340 | 0.191 | 0.110 |
| | 4 | 3 | 2.4100 | 2.3800 | 2.4100 | 0.0700 | 0.0404 |
| | 5 | 3 | 2.3367 | 2.3200 | 2.3367 | 0.1557 | 0.0899 |
| lambda | 1 | 3 | 0.2433 | 0.2300 | 0.2433 | 0.0808 | 0.0467 |
| | 2 | 3 | 0.2333 | 0.2000 | 0.2333 | 0.0577 | 0.0333 |
| | 3 | 3 | 0.2500 | 0.2400 | 0.2500 | 0.0557 | 0.0321 |
| | 4 | 3 | 0.21667 | 0.22000 | 0.21667 | 0.00577 | 0.00333 |
| | 5 | 3 | 0.2467 | 0.2600 | 0.2467 | 0.0416 | 0.0240 |
| even | 1 | 3 | 0.8300 | 0.8100 | 0.8300 | 0.1114 | 0.0643 |
| | 2 | 3 | 0.8500 | 0.8800 | 0.8500 | 0.0700 | 0.0404 |
| | 3 | 3 | 0.7867 | 0.7700 | 0.7867 | 0.0862 | 0.0498 |
| | 4 | 3 | 0.8867 | 0.9100 | 0.8867 | 0.0493 | 0.0285 |
| | 5 | 3 | 0.8367 | 0.8500 | 0.8367 | 0.0611 | 0.0353 |

**2YL4**

| Variable | trt | N | Mean | Median | TrMean | StDev | SEMean |
|---|---|---|---|---|---|---|---|
| no sp | 1 | 3 | 6.00 | 5.00 | 6.00 | 1.73 | 1.00 |
| | 2 | 3 | 6.333 | 6.000 | 6.333 | 0.577 | 0.333 |
| | 3 | 3 | 6.667 | 7.000 | 6.667 | 0.577 | 0.333 |
| | 4 | 3 | 9.67 | 8.00 | 9.67 | 3.79 | 2.19 |
| | 5 | 3 | 6.67 | 7.00 | 6.67 | 2.52 | 1.45 |
| indiv | 1 | 3 | 21.00 | 24.00 | 21.00 | 10.82 | 6.24 |
| | 2 | 3 | 20.00 | 22.00 | 20.00 | 4.36 | 2.52 |
| | 3 | 3 | 31.00 | 22.00 | 31.00 | 16.46 | 9.50 |
| | 4 | 3 | 28.3 | 17.0 | 28.3 | 22.3 | 12.9 |
| | 5 | 3 | 27.33 | 33.00 | 27.33 | 11.59 | 6.69 |
| hpr | 1 | 3 | 2.193 | 2.200 | 2.193 | 0.300 | 0.173 |
| | 2 | 3 | 2.340 | 2.340 | 2.340 | 0.320 | 0.185 |
| | 3 | 3 | 2.0767 | 1.9900 | 2.0767 | 0.1677 | 0.0968 |
| | 4 | 3 | 2.6933 | 2.7300 | 2.6933 | 0.0723 | 0.0418 |
| | 5 | 3 | 2.207 | 2.090 | 2.207 | 0.359 | 0.208 |
| lambda | 1 | 3 | 0.2600 | 0.2300 | 0.2600 | 0.0608 | 0.0351 |
| | 2 | 3 | 0.2333 | 0.2200 | 0.2333 | 0.0709 | 0.0410 |
| | 3 | 3 | 0.3167 | 0.3300 | 0.3167 | 0.0709 | 0.0410 |
| | 4 | 3 | 0.1967 | 0.1800 | 0.1967 | 0.0289 | 0.0167 |
| | 5 | 3 | 0.2833 | 0.2800 | 0.2833 | 0.1050 | 0.0606 |
| even | 1 | 3 | 0.8633 | 0.8300 | 0.8633 | 0.0757 | 0.0437 |
| | 2 | 3 | 0.8767 | 0.9000 | 0.8767 | 0.0874 | 0.0504 |
| | 3 | 3 | 0.7633 | 0.7100 | 0.7633 | 0.1012 | 0.0584 |
| | 4 | 3 | 0.8533 | 0.9100 | 0.8533 | 0.1159 | 0.0669 |
| | 5 | 3 | 0.8500 | 0.9300 | 0.8500 | 0.1652 | 0.0954 |

**3YH1**

| Variable | treatmt | N | Mean | Median | TrMean | StDev | SEMean |
|---|---|---|---|---|---|---|---|
| sp | 1 | 3 | 0.00000 | 0.00000 | 0.00000 | 0.00000 | 0.00000 |
| | 2 | 3 | 9.33 | 12.00 | 9.33 | 4.62 | 2.67 |
| | 3 | 3 | 6.33 | 9.00 | 6.33 | 5.51 | 3.18 |
| | 4 | 3 | 8.00 | 7.00 | 8.00 | 3.61 | 2.08 |
| | 5 | 3 | 9.00 | 9.00 | 9.00 | 2.00 | 1.15 |
| n | 1 | 3 | 0.00000 | 0.00000 | 0.00000 | 0.00000 | 0.00000 |
| | 2 | 3 | 18.00 | 24.00 | 18.00 | 12.17 | 7.02 |
| | 3 | 3 | 9.33 | 10.00 | 9.33 | 9.02 | 5.21 |
| | 4 | 3 | 14.67 | 9.00 | 14.67 | 13.43 | 7.75 |
| | 5 | 3 | 23.67 | 21.00 | 23.67 | 7.37 | 4.26 |
| h prime | 1 | 3 | 0.00000 | 0.00000 | 0.00000 | 0.00000 | 0.00000 |
| | 2 | 3 | 2.747 | 3.040 | 2.747 | 0.652 | 0.376 |
| | 3 | 3 | 2.06 | 3.06 | 2.06 | 1.78 | 1.03 |
| | 4 | 3 | 2.810 | 2.730 | 2.810 | 0.535 | 0.309 |
| | 5 | 3 | 2.717 | 2.750 | 2.717 | 0.192 | 0.111 |
| lambda | 1 | 3 | 0.00000 | 0.00000 | 0.00000 | 0.00000 | 0.00000 |
| | 2 | 3 | 0.1867 | 0.1700 | 0.1867 | 0.0569 | 0.0328 |
| | 3 | 3 | 0.0867 | 0.1200 | 0.0867 | 0.0757 | 0.0437 |
| | 4 | 3 | 0.1567 | 0.1600 | 0.1567 | 0.0451 | 0.0260 |
| | 5 | 3 | 0.1967 | 0.2000 | 0.1967 | 0.0351 | 0.0203 |
| e | 1 | 3 | 0.00000 | 0.00000 | 0.00000 | 0.00000 | 0.00000 |
| | 2 | 3 | 0.9133 | 0.8900 | 0.9133 | 0.0777 | 0.0448 |
| | 3 | 3 | 0.633 | 0.920 | 0.633 | 0.549 | 0.317 |
| | 4 | 3 | 0.9700 | 0.9700 | 0.9700 | 0.0300 | 0.0173 |
| | 5 | 3 | 0.8633 | 0.8900 | 0.8633 | 0.0643 | 0.0371 |

**3YH2**

| Variable | treatmt | N | Mean | Median | TrMean | StDev | SEMean |
|---|---|---|---|---|---|---|---|
| sp | 1 | 3 | 12.667 | 13.000 | 12.667 | 1.528 | 0.882 |
| | 2 | 3 | 13.67 | 14.00 | 13.67 | 2.52 | 1.45 |
| | 3 | 3 | 12.67 | 14.00 | 12.67 | 3.21 | 1.86 |
| | 4 | 3 | 8.33 | 11.00 | 8.33 | 5.51 | 3.18 |
| | 5 | 3 | 11.00 | 11.00 | 11.00 | 2.00 | 1.15 |
| n | 1 | 3 | 69.67 | 69.00 | 69.67 | 9.02 | 5.21 |
| | 2 | 3 | 73.0 | 58.0 | 73.0 | 43.5 | 25.1 |
| | 3 | 3 | 40.67 | 39.00 | 40.67 | 13.58 | 7.84 |
| | 4 | 3 | 21.33 | 28.00 | 21.33 | 12.42 | 7.17 |
| | 5 | 3 | 33.0 | 20.0 | 33.0 | 27.9 | 16.1 |
| h prime | 1 | 3 | 2.9033 | 2.9000 | 2.9033 | 0.1350 | 0.0780 |
| | 2 | 3 | 2.960 | 2.950 | 2.960 | 0.405 | 0.234 |
| | 3 | 3 | 3.107 | 3.130 | 3.107 | 0.386 | 0.223 |
| | 4 | 3 | 2.270 | 2.850 | 2.270 | 1.110 | 0.641 |
| | 5 | 3 | 2.930 | 2.920 | 2.930 | 0.445 | 0.257 |
| lambda | 1 | 3 | 0.1900 | 0.1900 | 0.1900 | 0.0400 | 0.0231 |
| | 2 | 3 | 0.1867 | 0.1600 | 0.1867 | 0.0737 | 0.0426 |
| | 3 | 3 | 0.1633 | 0.1700 | 0.1633 | 0.0404 | 0.0233 |
| | 4 | 3 | 0.297 | 0.190 | 0.297 | 0.185 | 0.107 |
| | 5 | 3 | 0.1900 | 0.1500 | 0.1900 | 0.1153 | 0.0666 |
| e | 1 | 3 | 0.8000 | 0.7900 | 0.8000 | 0.0755 | 0.0436 |
| | 2 | 3 | 0.7867 | 0.8400 | 0.7867 | 0.1012 | 0.0584 |
| | 3 | 3 | 0.8533 | 0.8500 | 0.8533 | 0.0351 | 0.0203 |
| | 4 | 3 | 0.8800 | 0.8300 | 0.8800 | 0.0954 | 0.0551 |
| | 5 | 3 | 0.8567 | 0.9200 | 0.8567 | 0.1644 | 0.0949 |

**3YH3**

| Variable | treatmt | N | Mean | Median | TrMean | StDev | SEMean |
|---|---|---|---|---|---|---|---|
| sp | 1 | 3 | 7.000 | 7.000 | 7.000 | 1.000 | 0.577 |
| | 2 | 3 | 6.67 | 6.00 | 6.67 | 2.08 | 1.20 |
| | 3 | 3 | 12.333 | 12.000 | 12.333 | 0.577 | 0.333 |
| | 4 | 3 | 9.667 | 9.000 | 9.667 | 1.155 | 0.667 |
| | 5 | 3 | 9.33 | 8.00 | 9.33 | 3.21 | 1.86 |
| n | 1 | 3 | 12.67 | 13.00 | 12.67 | 2.52 | 1.45 |
| | 2 | 3 | 11.67 | 10.00 | 11.67 | 4.73 | 2.73 |
| | 3 | 3 | 35.67 | 38.00 | 35.67 | 12.66 | 7.31 |
| | 4 | 3 | 18.67 | 18.00 | 18.67 | 5.03 | 2.91 |
| | 5 | 3 | 17.00 | 17.00 | 17.00 | 5.00 | 2.89 |
| h prime | 1 | 3 | 2.6333 | 2.7200 | 2.6333 | 0.1589 | 0.0917 |
| | 2 | 3 | 2.487 | 2.320 | 2.487 | 0.435 | 0.251 |
| | 3 | 3 | 3.213 | 3.270 | 3.213 | 0.230 | 0.133 |
| | 4 | 3 | 3.023 | 2.990 | 3.023 | 0.242 | 0.140 |
| | 5 | 3 | 3.000 | 2.860 | 3.000 | 0.428 | 0.247 |
| lambda | 1 | 3 | 0.1800 | 0.1800 | 0.1800 | 0.0200 | 0.0115 |
| | 2 | 3 | 0.2100 | 0.2400 | 0.2100 | 0.0608 | 0.0351 |
| | 3 | 3 | 0.1367 | 0.1300 | 0.1367 | 0.0404 | 0.0233 |
| | 4 | 3 | 0.1467 | 0.1400 | 0.1467 | 0.0306 | 0.0176 |
| | 5 | 3 | 0.1400 | 0.1500 | 0.1400 | 0.0361 | 0.0208 |
| e | 1 | 3 | 0.9433 | 0.9500 | 0.9433 | 0.0306 | 0.0176 |
| | 2 | 3 | 0.9233 | 0.9300 | 0.9233 | 0.0208 | 0.0120 |
| | 3 | 3 | 0.8867 | 0.9100 | 0.8867 | 0.0777 | 0.0448 |
| | 4 | 3 | 0.9233 | 0.9400 | 0.9233 | 0.0379 | 0.0219 |
| | 5 | 3 | 0.94667 | 0.95000 | 0.94667 | 0.00577 | 0.00333 |

**3YH4**

| Variable | treatmt | N | Mean | Median | TrMean | StDev | SEMean |
|---|---|---|---|---|---|---|---|
| sp | 1 | 3 | 7.667 | 8.000 | 7.667 | 1.528 | 0.882 |
| | 2 | 3 | 11.33 | 10.00 | 11.33 | 4.16 | 2.40 |
| | 3 | 3 | 13.00 | 14.00 | 13.00 | 2.65 | 1.53 |
| | 4 | 3 | 9.33 | 10.00 | 9.33 | 2.08 | 1.20 |
| | 5 | 3 | 9.67 | 9.00 | 9.67 | 2.08 | 1.20 |
| n | 1 | 3 | 14.667 | 15.000 | 14.667 | 0.577 | 0.333 |
| | 2 | 3 | 31.67 | 28.00 | 31.67 | 10.97 | 6.33 |
| | 3 | 3 | 35.33 | 31.00 | 35.33 | 12.10 | 6.98 |
| | 4 | 3 | 24.33 | 22.00 | 24.33 | 12.66 | 7.31 |
| | 5 | 3 | 19.000 | 19.000 | 19.000 | 1.000 | 0.577 |
| h prime | 1 | 3 | 2.727 | 2.710 | 2.727 | 0.325 | 0.188 |
| | 2 | 3 | 2.907 | 2.690 | 2.907 | 0.672 | 0.388 |
| | 3 | 3 | 3.167 | 3.420 | 3.167 | 0.492 | 0.284 |
| | 4 | 3 | 2.920 | 2.820 | 2.920 | 0.361 | 0.208 |
| | 5 | 3 | 3.017 | 2.930 | 3.017 | 0.358 | 0.207 |
| lambda | 1 | 3 | 0.1700 | 0.1800 | 0.1700 | 0.0361 | 0.0208 |
| | 2 | 3 | 0.1933 | 0.2000 | 0.1933 | 0.0902 | 0.0521 |
| | 3 | 3 | 0.1533 | 0.1200 | 0.1533 | 0.0666 | 0.0384 |
| | 4 | 3 | 0.1567 | 0.1800 | 0.1567 | 0.0404 | 0.0233 |
| | 5 | 3 | 0.1467 | 0.1500 | 0.1467 | 0.0351 | 0.0203 |
| e | 1 | 3 | 0.9300 | 0.9300 | 0.9300 | 0.0300 | 0.0173 |
| | 2 | 3 | 0.8367 | 0.8100 | 0.8367 | 0.0643 | 0.0371 |
| | 3 | 3 | 0.8567 | 0.8900 | 0.8567 | 0.0666 | 0.0384 |
| | 4 | 3 | 0.9133 | 0.9300 | 0.9133 | 0.0569 | 0.0328 |
| | 5 | 3 | 0.9233 | 0.9200 | 0.9233 | 0.0252 | 0.0145 |

**3YL1**

| Variable | trt | N | Mean | Median | TrMean | StDev | SEMean |
|---|---|---|---|---|---|---|---|
| no sp | 1 | 3 | 9.33 | 11.00 | 9.33 | 2.89 | 1.67 |
| | 2 | 3 | 8.333 | 8.000 | 8.333 | 0.577 | 0.333 |
| | 3 | 3 | 6.33 | 7.00 | 6.33 | 3.06 | 1.76 |
| | 4 | 3 | 6.00 | 7.00 | 6.00 | 2.65 | 1.53 |
| | 5 | 3 | 4.000 | 4.000 | 4.000 | 1.000 | 0.577 |
| indiv | 1 | 3 | 126.0 | 121.0 | 126.0 | 87.6 | 50.6 |
| | 2 | 3 | 109.3 | 81.0 | 109.3 | 50.8 | 29.3 |
| | 3 | 3 | 38.3 | 41.0 | 38.3 | 29.1 | 16.8 |
| | 4 | 3 | 63.3 | 77.0 | 63.3 | 47.0 | 27.1 |
| | 5 | 3 | 8.00 | 9.00 | 8.00 | 1.73 | 1.00 |
| hpr | 1 | 3 | 1.560 | 1.380 | 1.560 | 0.495 | 0.286 |
| | 2 | 3 | 1.967 | 1.810 | 1.967 | 0.399 | 0.230 |
| | 3 | 3 | 1.597 | 1.650 | 1.597 | 0.512 | 0.296 |
| | 4 | 3 | 1.543 | 1.630 | 1.543 | 0.407 | 0.235 |
| | 5 | 3 | 1.630 | 1.790 | 1.630 | 0.358 | 0.207 |
| lamb | 1 | 3 | 0.5133 | 0.5200 | 0.5133 | 0.1501 | 0.0867 |
| | 2 | 3 | 0.3500 | 0.4000 | 0.3500 | 0.0954 | 0.0551 |
| | 3 | 3 | 0.4633 | 0.4800 | 0.4633 | 0.1358 | 0.0784 |
| | 4 | 3 | 0.4833 | 0.5100 | 0.4833 | 0.1026 | 0.0593 |
| | 5 | 3 | 0.4000 | 0.3600 | 0.4000 | 0.0964 | 0.0557 |
| even | 1 | 3 | 0.4933 | 0.5300 | 0.4933 | 0.1387 | 0.0801 |
| | 2 | 3 | 0.6467 | 0.5700 | 0.6467 | 0.1415 | 0.0817 |
| | 3 | 3 | 0.6433 | 0.6700 | 0.6433 | 0.1124 | 0.0649 |
| | 4 | 3 | 0.6367 | 0.6800 | 0.6367 | 0.0839 | 0.0484 |
| | 5 | 3 | 0.8267 | 0.8100 | 0.8267 | 0.0666 | 0.0384 |

**3YL2**

| Variable | trt | N | Mean | Median | TrMean | StDev | SEMean |
|---|---|---|---|---|---|---|---|
| no sp | 1 | 3 | 8.000 | 8.000 | 8.000 | 1.000 | 0.577 |
| | 2 | 3 | 8.00 | 7.00 | 8.00 | 2.65 | 1.53 |
| | 3 | 3 | 8.333 | 9.000 | 8.333 | 1.155 | 0.667 |
| | 4 | 3 | 10.000 | 10.000 | 10.000 | 1.000 | 0.577 |
| | 5 | 3 | 8.67 | 7.00 | 8.67 | 3.79 | 2.19 |
| indiv | 1 | 3 | 58.67 | 63.00 | 58.67 | 16.92 | 9.77 |
| | 2 | 3 | 44.33 | 37.00 | 44.33 | 14.47 | 8.35 |
| | 3 | 3 | 80.3 | 88.0 | 80.3 | 18.7 | 10.8 |
| | 4 | 3 | 46.33 | 49.00 | 46.33 | 8.33 | 4.81 |
| | 5 | 3 | 85.33 | 85.00 | 85.33 | 16.50 | 9.53 |
| hpr | 1 | 3 | 2.280 | 2.310 | 2.280 | 0.336 | 0.194 |
| | 2 | 3 | 2.487 | 2.330 | 2.487 | 0.343 | 0.198 |
| | 3 | 3 | 2.227 | 2.290 | 2.227 | 0.193 | 0.111 |
| | 4 | 3 | 2.8333 | 2.8200 | 2.8333 | 0.0808 | 0.0467 |
| | 5 | 3 | 2.013 | 2.200 | 2.013 | 0.359 | 0.207 |
| lamb | 1 | 3 | 0.2833 | 0.2800 | 0.2833 | 0.0850 | 0.0491 |
| | 2 | 3 | 0.2233 | 0.2300 | 0.2233 | 0.0503 | 0.0291 |
| | 3 | 3 | 0.2833 | 0.2600 | 0.2833 | 0.0493 | 0.0285 |
| | 4 | 3 | 0.1800 | 0.1700 | 0.1800 | 0.0173 | 0.0100 |
| | 5 | 3 | 0.3600 | 0.3700 | 0.3600 | 0.1153 | 0.0666 |
| even | 1 | 3 | 0.7633 | 0.7300 | 0.7633 | 0.0945 | 0.0546 |
| | 2 | 3 | 0.8433 | 0.8300 | 0.8433 | 0.0513 | 0.0296 |
| | 3 | 3 | 0.7300 | 0.7200 | 0.7300 | 0.0173 | 0.0100 |
| | 4 | 3 | 0.8567 | 0.8500 | 0.8567 | 0.0306 | 0.0176 |
| | 5 | 3 | 0.6700 | 0.6200 | 0.6700 | 0.1136 | 0.0656 |

**3YL3**

| Variable | trt | N | Mean | Median | TrMean | StDev | SEMean |
|---|---|---|---|---|---|---|---|
| no sp | 1 | 3 | 7.333 | 8.000 | 7.333 | 1.155 | 0.667 |
| | 2 | 3 | 7.000 | 7.000 | 7.000 | 1.000 | 0.577 |
| | 3 | 3 | 6.333 | 6.000 | 6.333 | 1.528 | 0.882 |
| | 4 | 3 | 8.333 | 8.000 | 8.333 | 1.528 | 0.882 |
| | 5 | 3 | 6.333 | 6.000 | 6.333 | 1.528 | 0.882 |
| indiv | 1 | 3 | 53.7 | 53.0 | 53.7 | 23.0 | 13.3 |
| | 2 | 3 | 50.0 | 42.0 | 50.0 | 20.2 | 11.7 |
| | 3 | 3 | 26.00 | 28.00 | 26.00 | 13.11 | 7.57 |
| | 4 | 3 | 23.00 | 23.00 | 23.00 | 4.00 | 2.31 |
| | 5 | 3 | 33.00 | 36.00 | 33.00 | 7.00 | 4.04 |
| hpr | 1 | 3 | 2.3600 | 2.3500 | 2.3600 | 0.1652 | 0.0954 |
| | 2 | 3 | 2.297 | 2.380 | 2.297 | 0.333 | 0.192 |
| | 3 | 3 | 2.233 | 2.320 | 2.233 | 0.242 | 0.140 |
| | 4 | 3 | 2.650 | 2.620 | 2.650 | 0.346 | 0.200 |
| | 5 | 3 | 2.170 | 2.290 | 2.170 | 0.225 | 0.130 |
| lamb | 1 | 3 | 0.2367 | 0.2200 | 0.2367 | 0.0289 | 0.0167 |
| | 2 | 3 | 0.2633 | 0.2200 | 0.2633 | 0.0929 | 0.0536 |
| | 3 | 3 | 0.2700 | 0.2700 | 0.2700 | 0.0500 | 0.0289 |
| | 4 | 3 | 0.2067 | 0.1900 | 0.2067 | 0.0666 | 0.0384 |
| | 5 | 3 | 0.2733 | 0.2800 | 0.2733 | 0.0404 | 0.0233 |
| even | 1 | 3 | 0.8267 | 0.8400 | 0.8267 | 0.0907 | 0.0524 |
| | 2 | 3 | 0.8233 | 0.8600 | 0.8233 | 0.1193 | 0.0689 |
| | 3 | 3 | 0.8500 | 0.8400 | 0.8500 | 0.0458 | 0.0265 |
| | 4 | 3 | 0.8700 | 0.9100 | 0.8700 | 0.0872 | 0.0503 |
| | 5 | 3 | 0.8233 | 0.8200 | 0.8233 | 0.0551 | 0.0318 |

**3YL4**

| Variable | trt | N | Mean | Median | TrMean | StDev | SEMean |
|---|---|---|---|---|---|---|---|
| no sp | 1 | 3 | 6.667 | 6.000 | 6.667 | 1.155 | 0.667 |
| | 2 | 3 | 6.667 | 7.000 | 6.667 | 0.577 | 0.333 |
| | 3 | 3 | 6.333 | 6.000 | 6.333 | 1.528 | 0.882 |
| | 4 | 3 | 7.333 | 7.000 | 7.333 | 1.528 | 0.882 |
| | 5 | 3 | 5.00 | 5.00 | 5.00 | 2.00 | 1.15 |
| indiv | 1 | 3 | 61.7 | 65.0 | 61.7 | 27.2 | 15.7 |
| | 2 | 3 | 33.67 | 35.00 | 33.67 | 5.13 | 2.96 |
| | 3 | 3 | 20.00 | 21.00 | 20.00 | 4.58 | 2.65 |
| | 4 | 3 | 27.00 | 27.00 | 27.00 | 12.00 | 6.93 |
| | 5 | 3 | 18.67 | 18.00 | 18.67 | 11.02 | 6.36 |
| hpr | 1 | 3 | 1.9900 | 1.9600 | 1.9900 | 0.1277 | 0.0737 |
| | 2 | 3 | 2.2633 | 2.2100 | 2.2633 | 0.1102 | 0.0636 |
| | 3 | 3 | 2.057 | 2.150 | 2.057 | 0.516 | 0.298 |
| | 4 | 3 | 2.313 | 2.440 | 2.313 | 0.453 | 0.262 |
| | 5 | 3 | 1.823 | 1.720 | 1.823 | 0.386 | 0.223 |
| lamb | 1 | 3 | 0.3167 | 0.3200 | 0.3167 | 0.0252 | 0.0145 |
| | 2 | 3 | 0.2600 | 0.2700 | 0.2600 | 0.0265 | 0.0153 |
| | 3 | 3 | 0.3300 | 0.2900 | 0.3300 | 0.1345 | 0.0777 |
| | 4 | 3 | 0.2700 | 0.2000 | 0.2700 | 0.1300 | 0.0751 |
| | 5 | 3 | 0.3500 | 0.3800 | 0.3500 | 0.0794 | 0.0458 |
| even | 1 | 3 | 0.7333 | 0.7300 | 0.7333 | 0.0252 | 0.0145 |
| | 2 | 3 | 0.8300 | 0.8500 | 0.8300 | 0.0436 | 0.0252 |
| | 3 | 3 | 0.7733 | 0.8300 | 0.7733 | 0.1069 | 0.0617 |
| | 4 | 3 | 0.8100 | 0.8500 | 0.8100 | 0.1539 | 0.0889 |
| | 5 | 3 | 0.8300 | 0.8000 | 0.8300 | 0.1082 | 0.0624 |

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# *CHAPTER 3:*

# *EFFECTS OF AN ESTUARINE GRADIENT UPON PREDATOR-PREY DYNAMICS IN MARINE SOFT-SEDIMENT SYSTEMS: PREDATION INTENSITY ON* MACOMA BALTHICA

## *ABSTRACT*

This study represents a field test of the effects of a gradient in salinity on predation intensity on dominant macrobenthic species. The results are used to infer applicability of a consumer stress model on community regulation (Menge and Sutherland 1987) in this soft-bottom ecosystem. Specifically, I examined the effect of predation upon the survival of a key infaunal bivalve, *Macoma balthica*, that displays contrasting distribution and abundance patterns along an estuarine gradient. I also determined the abundance of major predators on *M. balthica* in the shallow habitats of the York River, a subestuary of Chesapeake Bay. Application of the consumer stress model in this system predicts that higher abundance of *M. balthica* in upriver zones is due to lower predator-induced mortality. Herein, I show that (1) natural abundance of shallow-water bivalves was higher upriver, similar to that in deep water populations, (2) both predation-induced mortality in field experiments as well as field measurements of natural mortality of clams were higher upriver, contrary to predictions of the consumer stress model, (3) predator abundance was greater upriver where predation intensity was higher, though size of predators was not significantly different between river zones, and (4) per-capita foraging efficiency on these bivalves was higher downriver. Hence, the observed patterns in diversity and environmental stress are in accord with a consumer stress model of community regulation, whereas the pattern in predator abundance and predation intensity (higher predation intensity in zones of higher environmental stress) is contrary to the model's predictions. The patterns in this soft-bottom ecosystem appear to be explained by an integration of a consumer stress model with a productivity model, resulting in a community governed through co-limitation by predators and resources.

# PREDATION INTENSITY ON *MACOMA BALTHICA*

## *INTRODUCTION*

Shallow-water soft-bottom habitats are dominated by predators capable of consuming a variety of prey (Virnstein 1977, 1979, Peterson 1979, Levinton 1982, Dayton 1984, Livingston 1984, Hines et al. 1990). Such predators can affect the structure of soft-bottom communities and persistence of populations (Peterson 1979, Schoener 1983, Commito and Ambrose 1985, Reise 1978, 1985, Sih et al. 1985, Hines et al. 1990, Wilson 1991). The impact of predators varies along gradients of environmental stress in both hard and soft-bottom systems (Menge and Sutherland 1987, Menge and Farrell 1989, Menge and Olson 1990).

In terrestrial and hard-bottom marine communities, the changing influence of structuring forces such as predation along gradients of environmental stress has been noted (Hairston et al. 1960, Connell 1961a, b, Paine 1966, Dayton 1971, Menge 1974, Menge and Sutherland 1987). One dominant environmental stress model which posits that consumers are more affected by environmental stress than prey is the Menge and Sutherland model (1987), a consumer stress model. This model, which was developed for the rocky intertidal habitat, predicts that for hard-bottom marine communities the effects of predation are inversely proportional to environmental stress, such that predation is most intense and influential under low stress. In contrast, the effect of environmental stress in modifying the role of biological factors such as predation has not been determined sufficiently for soft-bottom marine communities (Peterson 1979, Wilson 1991).

Competition and recruitment may not have as much influence upon community structure as predation and environmental stress in soft-bottom habitats, because of the three-dimensional nature of the sediment, which promotes coexistence of species and limits exclusion competition (Peterson 1979). Interference competition, however, can occur between infaunal polychaetes, affecting the foraging ability of competitors (Levin 1982). In general, in soft-bottom systems, interspecific competition appears less significant than other structuring forces (Peterson 1979, Dauer et al. 1982, Peterson 1982a, b, Wiltse et al. 1984, Peterson and Black 1988).

Environmental stress (i.e., conditions less than optimal for growth, reproduction or survival of individuals) can present itself either as direct physical stress, (e.g., mechanical force on organisms like wave shock or collisions with logs; Dayton 1971), or as physiological stress (e.g., abnormally high temperature, extreme salinity, reduced feeding time, or desiccation; Denny et al. 1985, Menge and Olson 1990). Consumer stress models predict that both types of stress can override a predator's feeding, reproduction or survival and thereby overshadow its impact upon prey species and community structure. Environmental factors known to affect growth rates and survival of estuarine organisms include temperature, pollutants, salinity, dissolved oxygen, and disease (Cadman and Weinstein 1977).

Physical stress is a dominant structuring force in hard-bottom marine habitats (Dayton 1971, Menge and Sutherland 1987). For example, the intertidal species *Hedophyllum sessile* is typically a competitive dominant except in wave-exposed physiologically optimal areas where *Lessoniopsis littoralis* is a much stronger dominant.

Physical forces may also be important in marine soft-bottom systems (Boesch 1977, Bonsdorff 1989, Mattila 1992). However, physiological stress may be more important in many shallow subtidal, soft-bottom systems, which are characterized by high seasonal variation in those abiotic factors, such as salinity, temperature and wave action, which can negatively impact physiological processes (Sanders 1969, Moore 1972, Menge 1975, Boesch 1977, Rosenberg 1977, Alongi 1990, Mattila 1992, Warwick and Clarke 1993). For example, in the Baltic where there are steep stress gradients (salinity, temperature, oxygen exposure, sediment quality), the abundance of benthos and fish are low and most species live toward the border of their physiological tolerance (Bonsdorff and Blomqvist 1993). Thus, in the northern Baltic Sea, the benthic community is largely structured by the harsh environment, and also by biotic interactions. In other systems, a continuous gradient in organics may be the primary example of environmental variability, with physical factors additionally contributing to the relative environmental harshness imposed on each species (Pearson and Rosenberg 1978). Thus, stress may play an important part in community regulation in shallow soft-bottom systems such as the tributaries of Chesapeake Bay.

Estuaries have sharp gradients in physical, geological and biological processes (Schaffner et al. 1987b) and salinity gradients are a pervasive feature of estuaries (Boesch 1971). In general, upriver low-salinity areas experience more extreme fluctuations in salinity, temperature, and turbidity than downriver high-salinity areas. For example, salinity changes during a tidal cycle in the upper estuary can be as high as 5 ppt within 12 hours, whereas less than 3 ppt change is common in the down-estuary areas (Boesch

1971). Long-term monitoring throughout Chesapeake Bay also shows that the variance in salinity (standard error of the mean) increases along with a decrease in salinity in the James, York, and Rappahannock Rivers (Dauer et al. 1989). In addition, temperature at the mouth of the York River is more stable than in the rest of the river because of the relative proximity to oceanic influence (Boesch 1971). Physical disturbance from sediment deposition is also greater upriver, usually near the turbidity maximum. The upriver areas of Chesapeake Bay tributaries have rapid sediment accumulation and sediments are physically structured, as compared to downriver areas that are more biologically reworked (Schaffner et al. 1987b). Along the gradients of salinity and associated stress, the role of predation has not been quantified in soft-bottom systems.

Models of structuring forces for marine benthos view 'top-down' factors (those factors from higher up in the food web) as most important in community regulation, i.e., most trophic levels below the top are predator-limited (Menge and Sutherland 1976, Hairston et al. 1960, Fretwell 1977, 1987, Oksanen et al. 1981). Thus predation is predicted to be important to regulating communities and populations.

Other investigators show only 'bottom-up' forces as important. These ideas are incorporated into Nutrient/Productivity Models (Menge and Olson 1990). For instance, all trophic levels are potentially limited by resource availability, and plants are not limited by herbivores except during extreme drought (White 1978). Other investigators show a combination of top-down and bottom-up forces as important (Getz 1984, Arditi and Ginzburg 1989, Posey et al. 1995). Processes on large scales may be governed by Nutrient/Productivity models, whereas those on local scales may be influenced by

environmental stress (Menge and Olson 1990). Therefore each system must be analyzed separately to determine which model is most appropriate. Although many factors likely affect species patterns, this study is designed to address only one of many important factors, predation, and to determine how the impact of predation on a population changes with stress.

The Menge and Sutherland model (1987) (MS), a consumer stress model (CSM) that incorporates environmental factors, posits that consumers are more severely affected by environmental stress than prey. This model supports the importance of top-down community structuring forces. Specifically, the MS model suggests that the importance of predation increases with reduced environmental stress in rocky intertidal systems, because of an increase in predator foraging efficiency in areas of lower stress (Fig. 3.1a; Menge and Lubchenco 1981, Gilinsky 1984, Menge and Sutherland 1976, 1987, Menge and Farrell 1989). For example, in areas of low wave exposure (low stress), the predatory starfish *Pisaster* is common and limits epifaunal prey density; in areas of extreme wave exposure and stress, its foraging activities and impact are minimal (Menge 1975). Thus, this consumer stress model predicts that the effect of predation on population density increases with decreasing stress. Such trends in predation over varying levels of environmental stress may also hold for soft-bottom communities (Sih et al. 1985).

In the soft-bottom system of the York River, the salinity gradient is associated with a change in diversity, and predation intensity may also change along this gradient (as in Menge and Sutherland's 1987 diversity model). In the estuary higher salinity zones have greater diversity (Boesch 1971). If upriver areas experience greater environmental

stress, then, based on diversity and stress characteristics, the York River system would be on the left half of Menge and Sutherland's diversity curve (points A to B, Fig. 3.1a). In experiments from hard-bottom systems, as diversity increases and stress decreases, the importance of predation increases. In the York River system, if the upriver salinity stress adversely affects consumers, predation intensity is predicted to decrease upriver, where diversity is low. Thus, if we examine a gradient in environmental stress, there are clear and testable predictions regarding the importance of predation along the gradient.

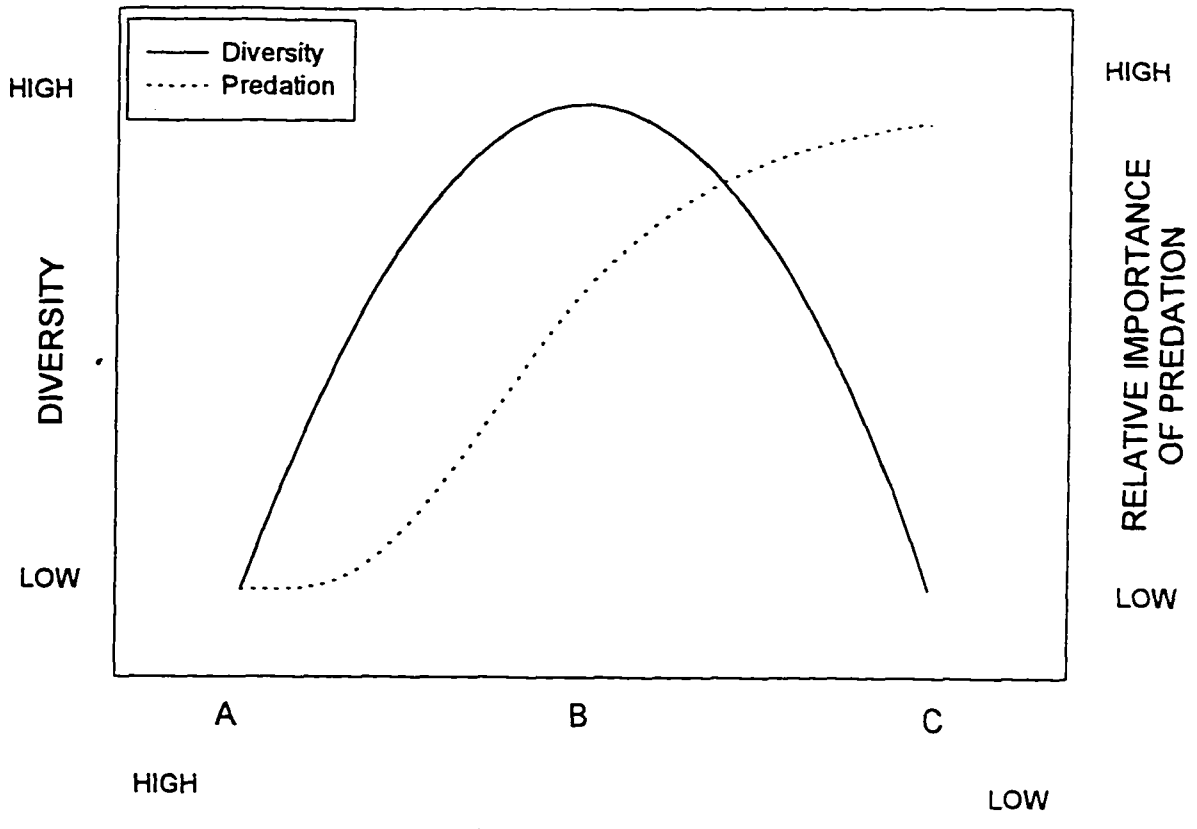
In this study, salinity is used as a surrogate measure to define an environmental gradient and test its impact upon predator-prey dynamics in marine soft-bottom systems (Menge and Olson 1990). Variation in predation intensity has not been investigated along salinity gradients, even though such gradients are a ubiquitous feature of estuaries (Boesch 1971).

Changes in physical characteristics are likely to have profound effects on the activities of resident fauna, such that lower salinity areas are more stressful (Menge and Olson 1990). This may be especially true in estuaries where many species are of marine origin (Remane and Schlieper 1971). Changing salinity requires osmoregulation which is costly in terms of energy expenditure, and low salinity may be additionally harsh for species with marine origins. Infauna are immobile and are evolutionarily adapted to their surrounding environmental fluctuations. Those that have evolved to endure the changing conditions remain resident in these low salinity areas.

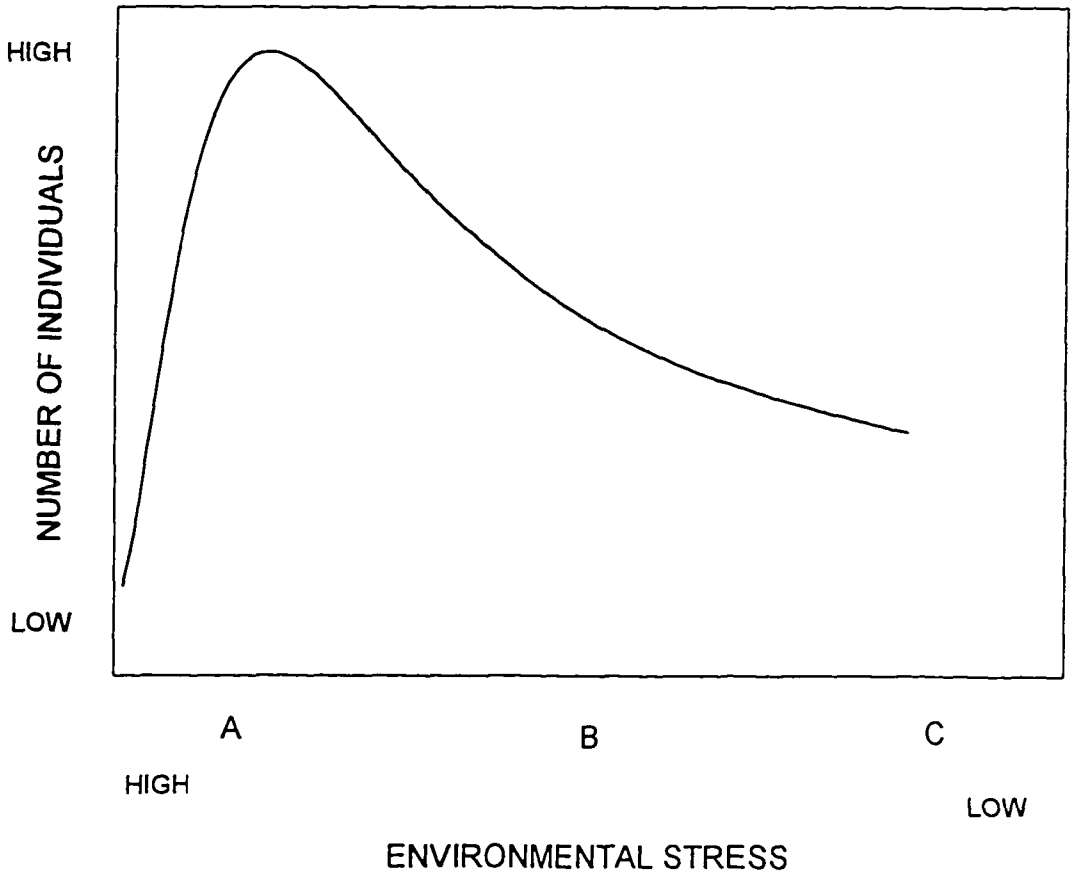
Conversely, predators are able to migrate, therefore they can escape undesirable environmental conditions and need not be physiologically adapted to a harsh environment.

Fig. 3.1 (a) Modification of the Menge and Sutherland (1987) consumer stress model showing the influence of predation along an environmental gradient and corresponding benthic community diversity. (b) Predicted densities of *Macoma balthica* along the same environmental gradient. At the far left (in fresh water, for example), environmental stress is so high that *M. balthica* does not survive. Compare three points along the curve: 'A' where environmental stress is severe, few species survive, thus diversity is low and the density of *Macoma balthica* is high; 'B' where environmental stress is intermediate, allowing more species to survive thus increasing diversity, yet predation is of little influence; 'C' where environmental stress is low but predation is severe, thus reducing both diversity and the density of most species, including *Macoma balthica*.

## PREDATION, DIVERSITY ENVIRONMENTAL STRESS




Macoma balthica




ENVIRONMENTAL STRESS

For instance, though the blue crab has a wide salinity tolerance (Mangum and Towle 1977), growth and feeding efficiency are higher at higher salinities (Cadman and Weinstein 1988). Though the blue crab is characterized as euryhaline, below suboptimal salinities (~27ppt), respiration rate increases (Colvocoresses et al. 1974, Mangum and Towle 1977) and varies inversely with salinity due to higher energy demands of osmotic regulation at low salinity (Findley et al. 1978). Temperature stress may also affect predators migrating into and out of upriver areas. For instance, ventilation rates in some estuarine fish (e.g., *Trinectes maculatus*, *Morone americana*, and *Leiostomus xanthurus*) significantly increased after temperature increases of 2.5 to 5°C (Burton 1979). Hence, I postulate that predators the impact of predation will be reduced in upriver, in higher stress.

***The Chesapeake Bay Predator-Prey System***

The Chesapeake Bay benthic community comprises diverse assemblages of species (Diaz and Schaffner 1990). Benthic infaunal distribution and abundance are associated with salinity gradients in addition to other physical factors such as sediment type, oxygen concentration, and frequency of bottom disturbance (Boesch et al. 1976, Schaffner et al. 1987a, Pihl et al. 1992). Predation appears to be a primary biotic factor influencing species abundances, at least in polyhaline-msohaline salinities (Virnstein 1977, Hines et al. 1990). Despite the extensive field and laboratory experiments conducted on the effects of predators on Chesapeake Bay benthic infauna (Virnstein 1977, Holland et al. 1980, Blundon and Kennedy 1982, Dauer et al. 1982, Hines et al. 1990, Mansour and Lipcius 1991, Pihl et al. 1992), variation in predation intensity across environmental gradients has

rarely been investigated in soft-bottom systems (Commito 1976), including latitudinal gradient effects (Virnstein et al. 1984), and oxygen gradient effects (Pihl et al. 1992).

In this study I use a dominant, benthic infaunal prey to test predation intensity along a salinity gradient. *Macoma balthica* (Mollusca: Bivalvia: Tellinidae) is a thin-shelled bivalve (up to 40 mm shell length) distributed in muddy and sandy sediments along both sides of the North Atlantic, and in the Pacific from the Gulf of Alaska to San Francisco Bay (Beukema and Meehan 1985, Martini and Morrison 1987). In Chesapeake Bay, *M. balthica* is a deposit-feeding and facultative suspension-feeding species that resides primarily in muddy habitats and can burrow to 40 cm in depth (Hines and Comtois 1985, Schaffner et al. 1987a, Hines et al. 1990). Settlement occurs in two pulses, a weak winter pulse and a large spring pulse in May, with abundances decreasing in late summer in conjunction with increased predator activity (Holland et al. 1980, 1987, Blundon and Kennedy 1982b, Holland 1985, Hines et al. 1990). Burial to depths >15 cm (Blundon and Kennedy 1982b, Ebersole and Kennedy 1995) as well as residence in low-density patches (Mansour and Lipcius 1991, Eggleston et al. 1992) may provide a refuge from predation for large juveniles and adults. *M. balthica* can serve as a primary food item for epibenthic crabs and fishes.

The abundance of *M. balthica* differs depending on location in the estuary. This species is characteristic of muddy or muddy-sand habitats in 5-25 ppt salinities (Beukema and Meehan 1985). The deep-water clam distribution can depend on both sediment type and oxygen stress. Most studies in York River tributaries show increasing abundances of *M. balthica* from downriver to upriver. For example, in the James River which does not

experience oxygen stress, few bivalves (mainly *M. balthica*) were found in deep-water lower mesohaline stations (~18 ppt) although there were some large *M. balthica* buried below 20 cm. However, abundances were maximum in the upper mesohaline (~ 5 ppt; Schaffner et al. 1987a). Additionally, long-term sampling showed similar patterns in the York River where densities of *M. balthica* were maximum in mesohaline regions, but dropped to zero in the polyhaline deep-water areas that suffer oxygen stress. Thus, all evidence from deep-water sampling show that the species is relatively rare in unvegetated high-salinity sites compared to low-salinity sites in the York River (Boesch 1977, Mansour 1992). There are several factors that could account for differential distribution including differences in recruitment, emigration or predation.

Recruitment is important to the abundance of *M. balthica*. Over ten years of monitoring data in a mesohaline site in the Maryland portion of Chesapeake Bay shows *M. balthica* abundances are influenced heavily by recruitment, as well as dissolved oxygen in deep water channels (Holland 1985). Large recruitment pulses accounted for much of the total variation in abundance. Year-to-year shifts in abundance were also correlated with year-to-year salinity fluctuations. Preliminary data on shallow water recruitment (Seitz and Lipcius, unpublished data) shows higher recruitment downriver over two sampling years. Thus differential recruitment does not appear to explain distribution of *M. balthica* throughout the river, although predation may be important.

Another important factor affecting distribution could be post-settlement dispersal. A secondary redistribution by juveniles in the plankton may lead to recolonization and consequent density fluctuations (Eagle 1975, Butman 1987). Juvenile *M. balthica* have

the ability to extend their byssus threads (thin mucus threads) into the water column where they can be carried by currents (Beukema et al. 1978, Beukema and de Vlas 1989). Juveniles as large as 14 mm length can also migrate using a floating behavior whereby they inflate their foot to become buoyant (Sorlin 1988). This method of transport may allow juveniles to find more suitable habitat than their original settlement habitat, although they are subject to surrounding water flow. Thus, final distribution of clams may be due to a combination of habitat and predation components.

Predation is postulated to be an important factor governing distribution of *M. balthica*. Intense predation by fish and crabs rapidly decrease abundances after recruitment pulses (Holland 1985), thus predation may influence seasonal distribution in shallow water (Holland et al. 1980, 1987). Abundances may be higher upriver as a result of higher predation downriver. The abundance of predators in deep water areas is greater upriver (Lipcius and Van Engel 1990; Chap. 2 - this dissertation), but, if predators are more stressed than prey, foraging efficiency may be reduced due to stress associated with the low-salinity habitat, as predicted by Menge and Sutherland's consumer stress model (1987).

The epibenthic predator guild is composed of several species including blue crabs (*Callinectes sapidus*), spot *(Leiostomus xanthurus*), croaker (*Micropogonias undulatus*), and hogchoker (*Trinectes maculatus*). The blue crab, a portunid crab, is dispersed widely along the Atlantic and Gulf coasts of North America, and is abundant throughout Chesapeake Bay (Williams 1984, Hines et al. 1987, 1990, Lipcius and Van Engel 1990). This species is important in energy transfer in estuaries, serving as both omnivore and prey

(Baird and Ulanowicz 1989). Feeding efficiency and prey capture in blue crabs vary significantly with prey availability, predator density and habitat complexity (Blundon and Kennedy 1982, Arnold 1984, Lipcius and Hines 1986, West and Williams 1986, Hines et al. 1990, Eggleston 1990, Mansour and Lipcius 1991, Eggleston et al. 1992). The diet of blue crabs, however, consists mainly of bivalve molluscs, predominantly *M. balthica* and *Mya arenaria*, and conspecifics, as well as polychaetes, other crabs and fish (Laughlin 1982, Alexander 1986, Hines et al. 1990, Mansour 1992, Ebersole and Kennedy 1995). Spot (*Leiostomus xanthurus*) and hogchoker (*Trinectes maculatus*) are common bottom-feeding fishes in southeast estuaries (Chao and Musick 1977). Such demersal finfish predators primarily browse on clam siphons, reducing the depth of clam penetration and making them more readily available to predators (Hines et al. 1990).

Infaunal predators are also present in this system, such as the polychaetes *Nereis succinea* and *Glycinde solitaria*, which are among the dominants in shallow water sampling (Chap. 2 - this dissertation). Downriver, higher salinities may allow for a greater diversity of infaunal predators such as nemerteans and gastropods that could potentially feed on newly recruited bivalves, affecting overall densities (Ambrose 1984).

***Rationale and hypotheses***

The consumer stress model (Menge and Sutherland 1987) posits that the effect of predation on the benthic community will decrease with increasing stress, and that diversity should have a unimodal peak along the stress gradient. A stress gradient exists in the York River whereby upriver, low-salinity zones have greater fluctuations in temperature,

salinity and turbidity and are therefore more stressful (Boesch 1977, Dauer et al 1993), similar to wave-exposed zones of the rocky intertidal where predators are scarce (Menge 1978). Diversity decreases with increasing stress upriver (Boesch 1977, Chap. 2 - this dissertation), similar to the exposed areas of the rocky intertidal where competitive mussels dominate in the absence of predation (Connell 1978). Predation could be similarly limited by stress upriver in this soft-bottom community.

*M. balthica* is a dominant infaunal dweller that is readily consumed by epibenthic predators (Diaz and Schaffner 1990, Hines et al. 1990, Pihl et al. 1992), and its abundance is substantially greater upriver (Mansour 1992), similar to the mussel *Mytilus californianus* which is a preferred prey of rocky intertidal starfish and whose abundance is greatest in stressful wave-exposed zones. Both the soft-bottom and hard-bottom patterns are consistent with the hypothesis that predation intensity is lower in more stressful areas. Thus, I propose that *M. balthica* can be used as a model species to detect differential predation along a stress gradient from upriver (high stress) to downriver (low stress).

This experiment therefore addresses the following hypotheses examining natural abundance of clams, the effect of predator-induced mortality on the clam *M. balthica*, and predator abundance in various zones in the York River differing by salinity. I predict that densities of *M. balthica* along a gradient from fresh water to oceanic water will follow a humped-shaped curve (Fig. 3.1b) as seen in deep-water densities (Dauer et al. 1989). In completely fresh water, where physiological stress is severe for marine species, only freshwater species thrive, and few *M. balthica* are present. The density of *M. balthica* is greater at slightly higher salinity, as they do well in low salinity. As environmental stress

decreases, predation increases, and the abundance of *M. balthica* decreases. Where environmental stress is low but predation is severe (at high salinity), the density of most species, including *M. balthica* is further reduced. In deep-water areas, the abundance of *M. balthica* is greater upriver than downriver (Schaffner et al. 1987a, Dauer et al. 1989, Mansour 1992), suggesting that the distribution throughout the system (in shallow-water areas) may follow the same trend, leading to $Ha_1$:

- **$Ho_1$: There are no trends in shallow water abundances of *M. balthica*,**

  **$Ha_1$: The natural abundance of clams in *shallow water* habitats is greater upriver (Fig. 3.1b);**

The consumer stress model predicts that the influence of predation decreases in areas of higher stress where diversity is relatively low (Boesch 1977, Holland et al. 1980, Chap. 2 - this dissertation), leading to $Ha_2$ and $Ha_3$:

- **$Ho_2$: There is no difference in the abundance of epibenthic predators upriver and downriver,**

  **$Ha_2$: The abundance of epibenthic predators in shallow water is lower in upriver zones (as predicted by a consumer stress model);**

- **$Ho_3$: There is no difference in efficiency (per-capita consumption of prey) of epibenthic predators in shallow water upriver vs. downriver**

  **$Ha_3$: The efficiency (per-capita consumption of prey) of epibenthic predators in shallow water is lower upriver, in higher stress zones;**

and therefore $Ha_4$:

- **$Ho_4$: There is no difference in predator-induced mortality of *M. balthica* upriver vs. downriver,**

  **$Ha_4$: Predator-induced mortality of *M. balthica* is lower in upriver zones.**

To test these hypotheses, I quantify natural abundance of *M. balthica* and its predators, natural mortality of *M. balthica*, and employ field experiments utilizing transplanted clams to assess predator-induced mortality for *M. balthica* in York upriver and downriver habitats.

## *METHODS AND MATERIALS*

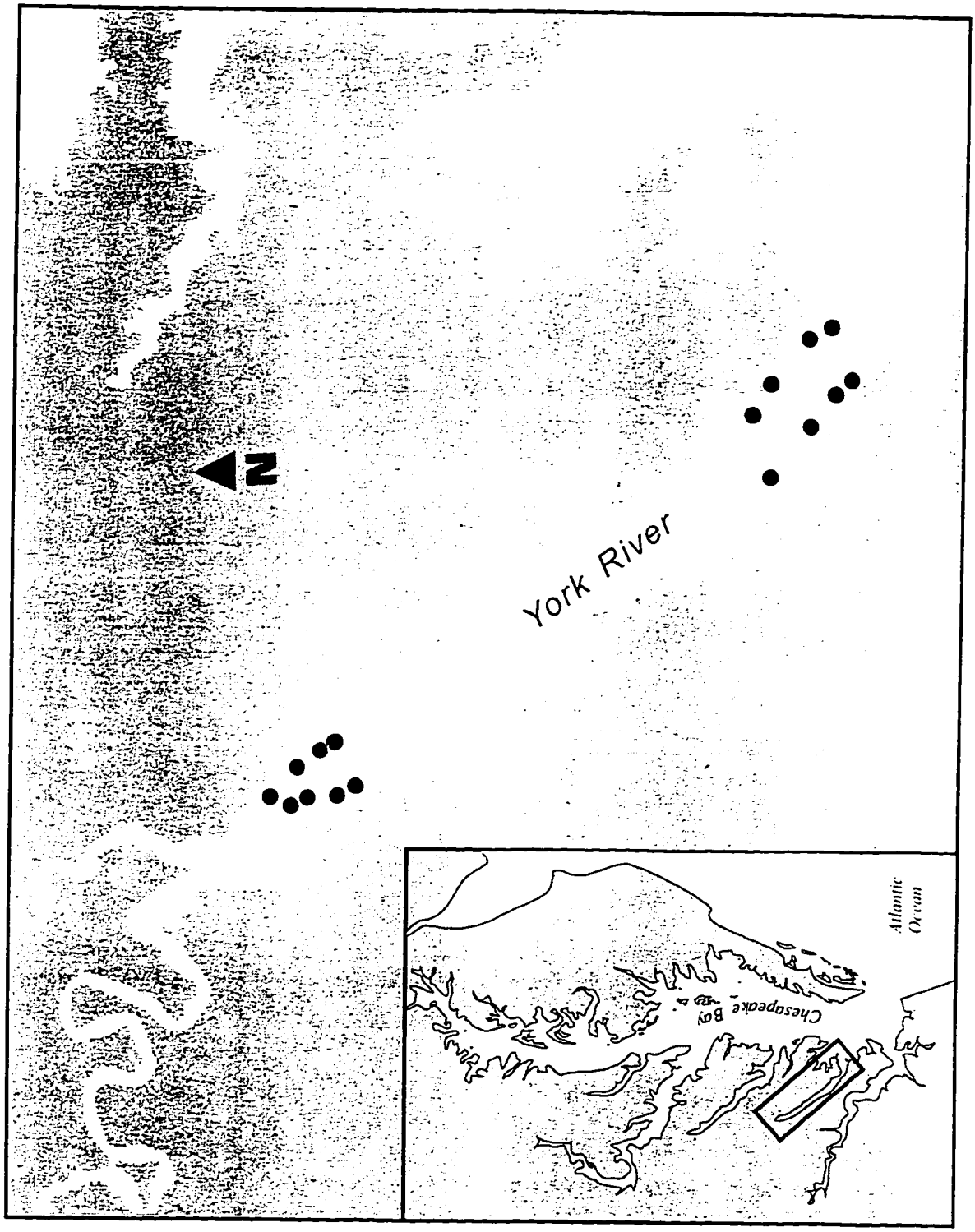
### *Study area*

This study was conducted in muddy-sand sediments of the shallow subtidal zone (1-2 m depth) in the York River, a tributary of Chesapeake Bay. Eight sites were set up randomly in each of two zones differing by location and salinity, the lower-mesohaline zone at about 5-10 ppt (upriver), and the upper-mesohaline zone at about 15-20 ppt (downriver). Upriver sites were approximately 40 km from the mouth of the York River and located near West Point, whereas the downriver sites were approximately 8 km from the mouth, near Gloucester Point (Fig. 3.2). Measured salinity varied significantly between the two zones (ANOVA, $P < 0.001$), upriver had lower salinity (mean = 8.8 ppt, range 5.0-10.0 ppt) and downriver had higher salinity (mean = 16.1 ppt, range 15.0-19.0 ppt). Particulate organic carbon was significantly higher upriver than downriver (ANOVA, df = 9, F = 6.24, $P = 0.037$ - Chap. 2 - this dissertation).

### *Natural clam density*

I quantified clam abundance in each of the eight sites per zone at the start of the first transplant experiment (week 0 and 1). At the time of clam transplanting (week 0), a PVC frame was placed on the sediment surface at each site marking a 0.25m$^2$ plot where natural clams were excavated to 30 cm depth using a suction dredge (Orth and van Montfrans 1987, Hines et al. 1990, Eggleston et al. 1992). This was placed approximately

Fig. 3.2. Map of the Virginia portion of Chesapeake Bay with experimental sites along the York River Upriver and Downriver denoted with black circles.



two meters away from the experimental plot at each replicate site. All bivalves in the suction samples were removed, identified, enumerated and total length was measured.

After seven days (week 1), when experimental plots were excavated, the frame was again deployed approximately two meters away from the experimental plots and another suction sample of natural clams was taken. Clam abundance between upriver and downriver zones was compared each time period using an Analysis of Variance (ANOVA) model with river zone as a fixed factor. Clam density between time periods was compared separately for upriver and downriver zones using a paired t-test with the difference in clam density at each site between time periods as the dependent variable. Dependent variables were log-transformed to meet assumptions of normality and homogeneity of variance (Underwood 1981).

*Natural clam mortality*

The best measure of natural mortality comes from following a group of individuals over time. To estimate natural mortality concurrent with the manipulative experiments, natural clam abundance between time periods (week 0 and week 1) was compared separately for upriver and downriver zones. The finite mortality rate ranges from 0 to 1 and was determined using the following equation (Krebs 1989):

- $m = 1 - (N_t/N_o)$ (1)

The instantaneous mortality rate ranges from 0 to negative infinity and was also determined:

- $i = \ln (N_t/N_o)$ (2)

where $N_t$ = number of individuals at end of time period t

$N_o$ = number of individuals alive at start of time period, $N_t/N_o$ = finite survival rate.

***Experimental clam mortality***

I tested the effect of predation by epibenthic crabs and fishes on *Macoma balthica* in two river zones in the field with three sets of experiments using transplants of clams in the summer of 1995. Large adult clams were used in transplant trial 1 (size range = 24.6 mm - 32.10 mm, mean 25.5), whereas small (range 10.1-16.8, mean 13.7 mm) and large (range 22.1-31.3, mean 24.5 mm) clams were transplanted at each site in subsequent trials. Clam sizes used in the experiments were based on random samples of clams collected from sediments in the area of the experimental plots.

Clams were collected from the upriver zone using a suction dredge, and slowly acclimated in the laboratory (over a 2-day period) to a salinity midway between that of upriver and downriver sites (approximately 10 ppt) at room temperature (~20°C). Before transplantation, the shell was dried and marked with an "x" using a permanent magic marker. At each site (Fig. 3.2), clams were carefully buried, foot down just below the sediment surface, relatively evenly-spaced, and taking care to leave the surrounding sediment intact. Salinity was recorded at each site.

After clams were transplanted, all plots were then covered with a predator exclusion cage (mesh size 13 mm) for an acclimation period of 48 h; previous laboratory trials indicated that 24 h was sufficient time for clams to achieve a stable burial depth (Mansour and Lipcius 1991, Eggleston et al. 1992). After acclimation, cages were removed from half of the plots (uncaged treatment), left on the other half (caged controls), and all plots were left intact for 7 days.

A the end of the exposure period, contents of all caged and uncaged plots were extracted to a depth of 30 cm using a suction dredge with a 1-mm mesh collection bag fitted to the outflow. Both marked and unmarked *M. balthica* and other clams were enumerated. Marked broken shells were noted as indicative of crab predation. Marked shells with no live individual were noted as evidence of physical/physiological or handling mortality. Physical/physiological mortality was significantly higher at the downriver sites (ANOVA, $df = 40$, $F = 9.49$, $P < 0.005$). Physical/physiological mortality did not differ not by time period (ANOVA, $df = 40$, $F = 3.33$, $P < 0.05$).

For each transplant experiment, I compared two river zones (upriver and downriver) with 8 sites divided among two treatments (caged control and uncaged experimental), and four replicates for Transplant 1 ($2 \times 2 \times 4 = 32$ plots). Half the sites were used for Transplants 2 and 3 and each site was either control or experimental. Transplants 2 and 3 had two replicates of each of two sizes ($2 \times 2 \times 2 = 16$ plots). Each plot consisted of a 0.5m x 0.5m ($0.25m^2$) area of sediment where 10 *M. balthica* were marked, measured and planted in the sediment. The plot was marked off with a frame deployed over two PVC stakes. After planting of the clams, the frame was removed to

minimize predator attraction. Transplant 1 was conducted on 17-24 July, Transplant 2 on 9-18 August, and Transplant 3 on 17-25 August.

For Transplant 2 and 3, two size classes of clams were planted at each site, small, and large. Of the 16 sites used in Transplant 1, cages were tampered with, and physical/physiological mortality was high at some sites. Of the better sites, four sites were chosen upriver and four downriver; two experimental and two control. There was no difference in ambient clam densities between those sites used and those discarded (Upriver: ANOVA, df = 7, MS = 145, F = 0.37, $P = 0.57$; Downriver: ANOVA, df = 7, MS = 2, F = 1.00, $P = 0.36$), thus clam abundance and mortality at sites chosen should be representative of all sites. At each site a plot of both large and small clams was established to allow paired comparisons.

In the plots with marked clams, at retrieval some marked clams were found live, some were found dead from physical/physiological mortality with two whole valves and umbo (handling + physical/physiological mortality), and some were missing (predation plus emigration). The 'missing' from the controls should account for emigration. Thus, the mean 'missing + physical' from the controls was subtracted from each 'missing' experimental to get predation-induced mortality.

The number of clams suffering predation did not differ by clam size (paired t-test, df = 7, d = 0.02 mm, 95% C.I. = -0.21 - 0.24), thus both size classes were pooled to give four replicates of each treatment (control and experimental) in each river zone. These replicates were used to compare mortality due to predation and physical factors by river zone. Additionally, to increase the power of the tests by elevating sample size,

Transplants 2 and 3 were pooled to compare effects of clam size. When predation was not significant by clam size, all three transplant experiments were pooled in an ANOVA with time as a blocking factor, and river zone as a fixed factor.

*Natural predator abundance*

Predator abundance in shallow water was quantified by trawling on 21-22 July, 1995 (though this was conducted over a short time frame, patterns are consistent throughout the summer; VIMS trawl survey). At each of the eight upriver and downriver sites, demersal fishes and crabs were collected with a 4.9-m semi-balloon otter trawl (3-m wide mouth, 5-cm-mesh net body, and 7-mm-mesh cod end). Two 2-min tows were taken parallel to shore at each site, one with the tidal current, and one against the tidal current. Both trawls were pooled and analyzed as one sample. Thus, four replicate samples were taken in each of the upriver and downriver zones. Although the estimate of predator abundance from trawling can be low due to gear avoidance by the predators (trawl efficiency for most predators is ~22%; Homer et al. 1980), all sizes of predators are caught with approximately equal efficiency except for extremely small individuals which can escape through the mesh (Homer et al. 1980). Animals in each trawl were identified, counted and measured (fish: total length, crabs: carapace width).

In addition to Pearson's correlations, a Multivariate Analysis of Variance (MANOVA) model was used to analyze predator abundance with species of fish or crabs defining the set of multivariate dependent variables, and river zone as a fixed factor (Underwood 1981). Because of significant heterogeneity in raw abundances, abundance

data was Log(x+1)-transformed for analyses. Variances in the Log(x+1)-transformed abundance data were homogeneous between river zones. Predator size between river zones was compared using multiple ANOVA models set at experiment-wise error rate of 0.05.

## *RESULTS*

### *Natural Clam Density and size structure*

Three clam species were collected within the 16 sites-- *Macoma balthica*, *M. mitchelli*, and *Tagelus plebeius*. Total natural clam density was significantly higher upriver than downriver (Fig. 3.3; Table 3.1). The Baltic clam, *M. balthica*, comprised 94-98% of all clams collected upriver, where its density declined from week 0 (mean abundance$\pm$SE = 128.0/m$^2$ $\pm$ 63.2) to week 1 (92.5/m$^2$ $\pm$ 22.0) (paired t-test; t = 2.39, df = 7, $P$ = 0.024). From these differences in abundance across weeks, finite survival rate for *M. balthica* upriver was calculated as 0.72 (72%), yielding a finite mortality of 28% per week. The corresponding instantaneous mortality rate ($\ln(N_t/N_0)$) was -0.32 for *M. balthica* upriver. There was no difference in abundance of clams other than *M. balthica* upriver (paired t-test, t = -0.55, df = 7, $P$ = 0.70). Few clams were collected downriver during either time period; there was no difference in the abundance of total clams between time periods downriver (paired t-test, t = -0.62, df = 7, $P$ = 0.72; Fig. 3.3).

There was a bimodal distribution in the mean size of ambient *M. balthica* collected in the eight upriver sites. At initial sampling, week 0, the mean length was 14.2 $\pm$ 0.3 mm for cohort 1 and 26.0 mm $\pm$ 0.4 mm for cohort 2 (Fig 3.4a), and at week 1 the mean length was 15.4 $\pm$ 0.2 mm for cohort 1 and 26.9 $\pm$ 0.6 mm for cohort 2 (Fig. 3.4b) though this difference in size was not significant (paired t-test, t = 0.28, df = 7, $P$ = 0.79).

Fig. 3.3. Mean abundance of all natural clams/$m^2$ in Upriver and Downriver zones at Week 0 (17-19 July 1995) and Week 1 (22-24 July). Significant differences ($P < 0.05$) are indicated with the asterisk, and means that are not significantly different ($P > 0.05$) are indicated with ns.

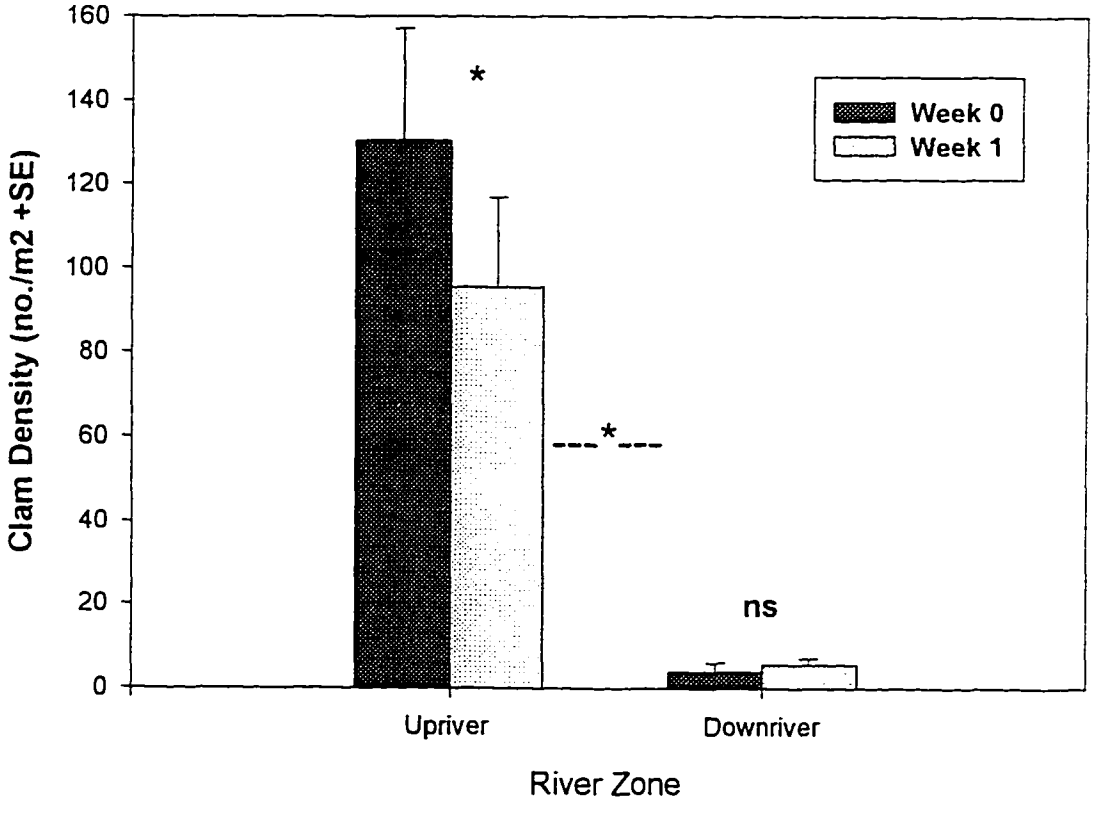
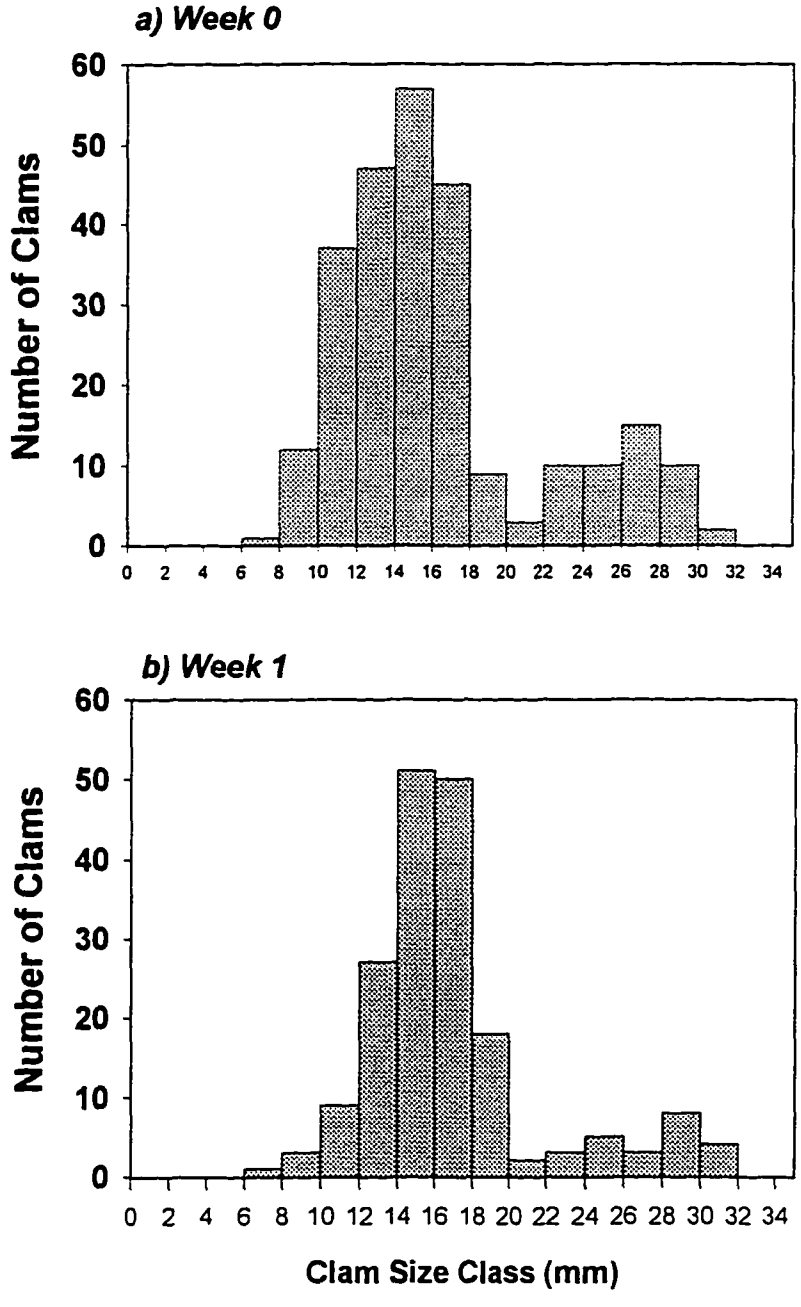


Table 3.1. Density of all clam species between zones in the York River. ANOVA used River zone (upriver and downriver) as a fixed factor; Time as a blocking factor using week 0 (July 17-19) and week 1 (July 24-26). The dependent variable was number of clams/$m^2$.

| Source of variation | SS | df | MS | F |
|---|---|---|---|---|
| River zone | 5852.3 | 1 | 5852.3 | 39.67**** |
| Time | 139.2 | 1 | 139.2 | $0.94^{ns}$ |
| Error | 4278.2 | 29 | 147.5 | |

**** $P < 0.001$; ns $P > 0.05$.

Fig. 3.4. Size-frequency of ambient *Macoma balthica* from (a) sampling period week 0 (17-19 July 1995) and (b) sampling period week 1 (22-24 July 1995). Size classes are at 2-mm intervals between even numbers.



***Experimental clam mortality - Size effects***

Only large clams were used in Transplant 1; marked clams transplanted in upriver vs. downriver sites did not differ in size (ANOVA, $F = 1.16$, $df = 159$, $P = 0.28$). The mean size of clams planted within experimental plots for Transplant 1 was $27.2 \pm 0.1$ mm, near the mode of the larger cohort identified in ambient clams (Fig 3.4). The mean size of surviving marked clams (mean = 26.8 mm) did not differ significantly from that of the initial marked clams (mean = 27.2 mm) (paired t-test, $t = 1.82$, $df = 21$, $P = 0.083$).

In Transplants 2 and 3, proportional mortality due to predation did not differ significantly by size (Fig. 3.5a, c, e; $P = 0.668$, Table 3.2a) nor did proportional mortality due to physical/physiological or handling stress (Fig. 3.5b, d, f; ANOVA, $df = 24$, $F = 0.15$, $P = 0.70$).

***Experimental clam mortality - Predation effects***

Because there was no significant difference in bivalve mortality by size, and no significant interaction of Size x Zone, data from both size classes were pooled. For all transplants, predation-induced mortality was significantly higher upriver (29%) than downriver (10%) (Fig. 3.6; Table 3.2). The mean predation-induced proportional mortality for experimental clams upriver was nearly equivalent to the finite mortality rate determined for natural clams (28%). Time as a blocking factor was not significant.

Fig. 3.5. Proportional mortality (mean/week + SE) of transplanted *Macoma balthica* from predation (a, c, e) and physiological factors (non-predatory mortality) (b, d, f) for three experimental trials. To arrive at predation-induced mortality, mean physiological mortality was subtracted from total mortality for each plot.

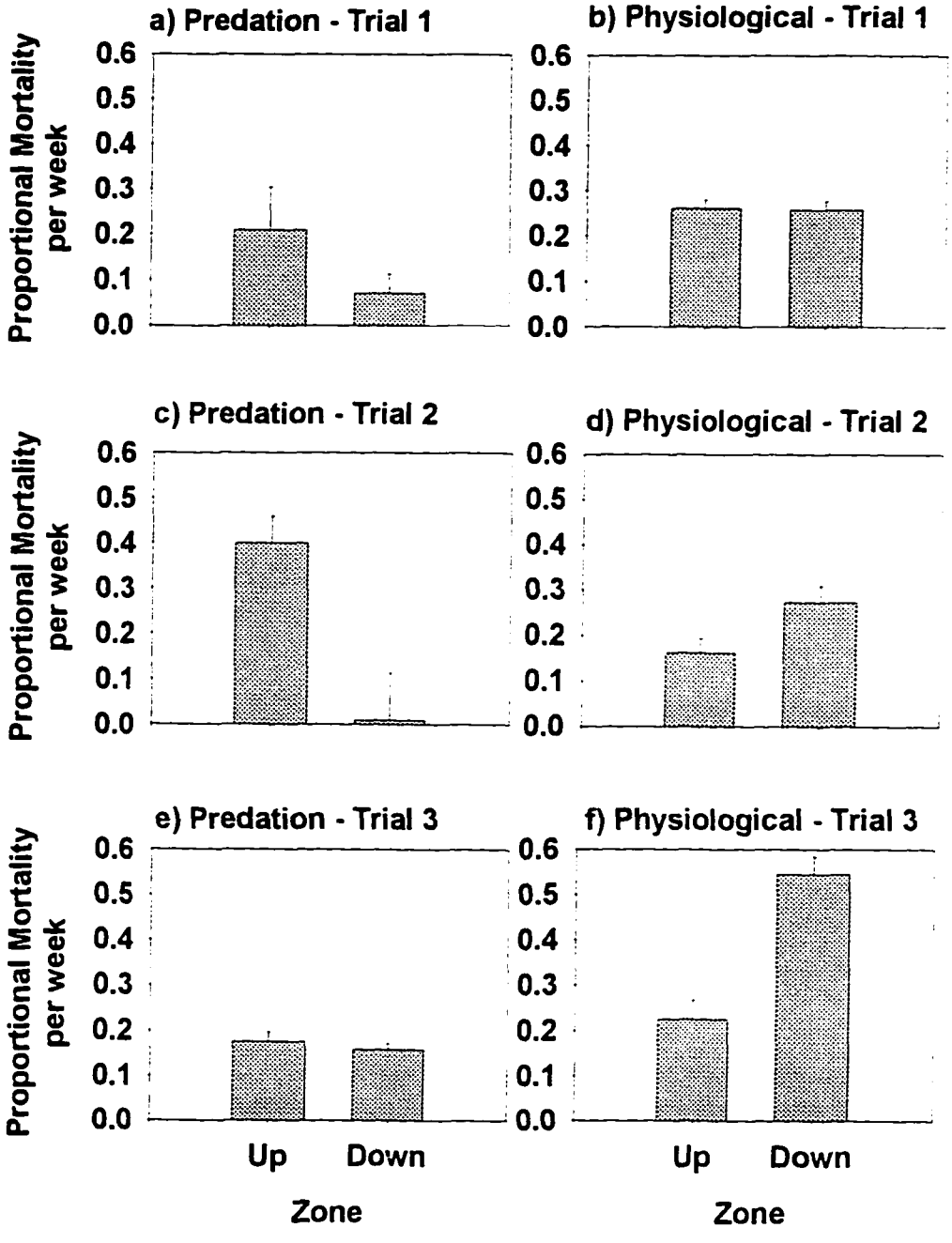
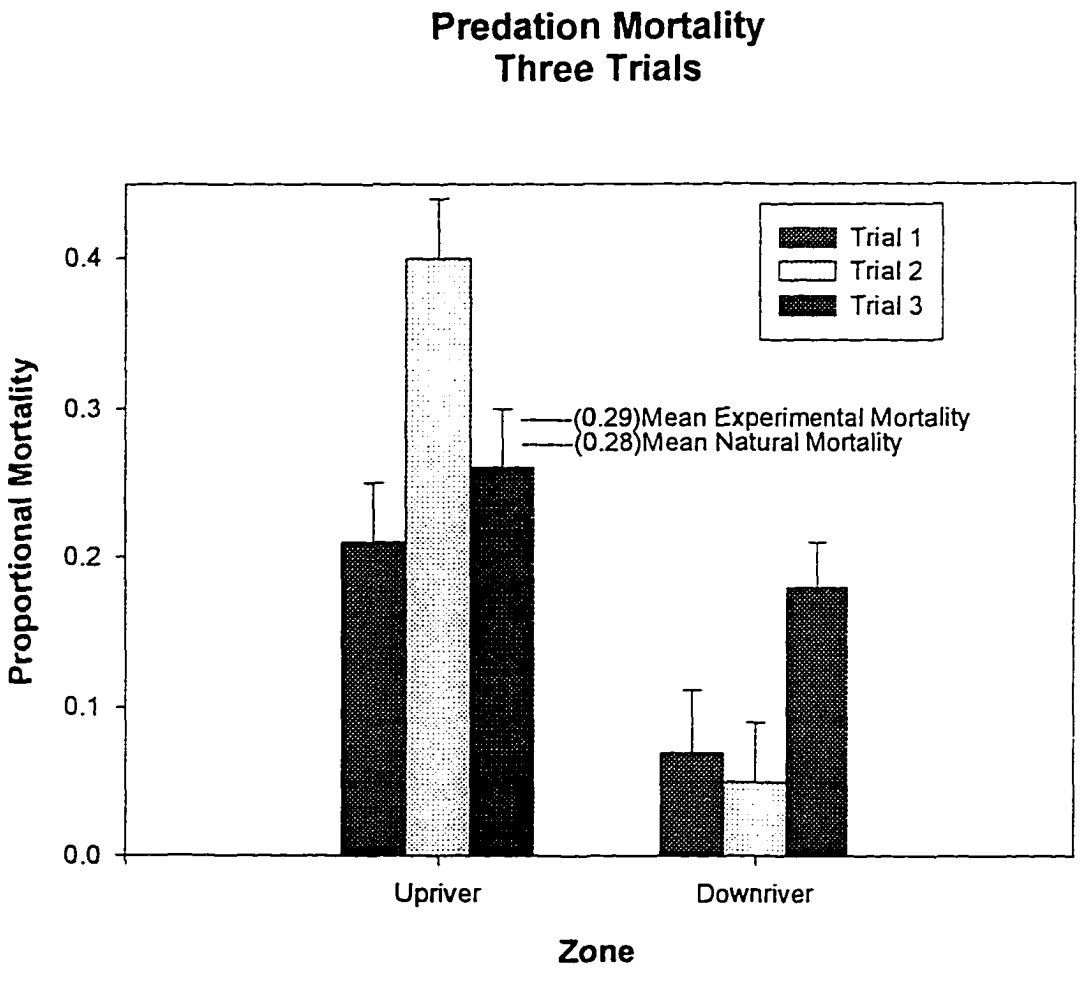


Table 3.2. Proportional mortality of transplanted clams due to predation between zones in the York River. ANOVA with (a) pooled data from Transplants 2 and 3, and (b) pooled data from all three Transplants with large and small clams pooled. Clam size (small and large -- for (a) only) and River zone (upriver and downriver) were fixed factors; time (Transplant 2 or 3) was a blocking factor.

| Category | Source of variation | SS | df | MS | F |
|---|---|---|---|---|---|
| Predation Mortality | Clam Size | 0.005 | 1 | 0.005 | $0.19^{ns}$ |
| (a) Transpl. 2 & 3 | River Zone | 0.192 | 1 | 0.192 | 6.69* |
| | Size x Zone | 0.010 | 1 | 0.010 | $0.35^{ns}$ |
| | Time | 0.000 | 1 | 0.000 | 0.00 |
| | Error | 0.344 | 12 | 0.029 | |
| Predation Mortality | River Zone | 0.212 | 1 | 0.212 | 8.65** |
| (b) All Transplants | Time | 0.040 | 2 | 0.040 | $0.82^{ns}$ |
| | Error | 0.493 | 20 | 0.024 | |

** $P < 0.01$; * $P < 0.05$; ns $P > 0.05$.

Fig. 3.6. Proportional mortality (mean mortality/week ± SE) of transplanted *Macoma balthica* due to predation Upriver and Downriver for three trials: Trial 1, 17-24 July; Trial 2, 9-18 August; and Trial 3, 15-25 August. Mean experimental mortality across all three trials and predator-induced mortality of natural clams are indicated with horizontal dashed lines.



***Natural predator abundance***

Epibenthic predators collected in shallow water trawls included the blue crab, *Callinectes sapidus*, various finfish including spot, *Leiostomus xanthurus*, croaker, *Micropogonias undulatus*, hogchoker, *Trinectes maculatus*, and white perch, *Morone sp.* A total of 799 epibenthic predators were caught, with hogchoker comprising 75.6% of the total, croaker 11.7%, crabs 6.8% , spot 3.2% , and other species 2.7%.

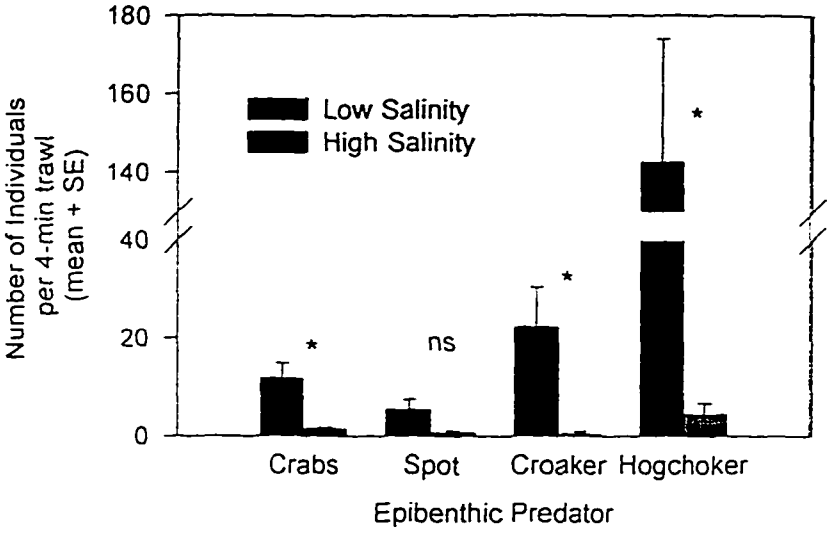
Significantly more blue crabs, spot, croaker and hogchoker were caught upriver than downriver (Fig. 3.7a; MANOVA, Table 3.3). There was a significant positive correlation in abundance between crabs and spot, croaker and hogchoker, and croaker and other uncommon epibenthic predators such as white perch (Table 3.4).

Predator size did not differ significantly between upriver and downriver zones for blue crabs (ANOVA, df = 31, F = 0.58, $P$=0.452), spot (ANOVA, df = 22, F = 1.13, $P$ = 0.301), and croaker (ANOVA, df = 90, F = 3.54, $P$ = 0.063)(Fig. 3.7b). Downriver, however, hogchoker were significantly larger than those upriver (Fig. 3.7b; ANOVA, df = 616, F = 24.37, P < 0.001 for log-transformed data). Individuals of each predator type were pooled across river zones and examined for patterns in size-frequencies. Crab and hogchoker populations showed a bimodal distribution of sizes (Fig. 3.8a, d), whereas there was a unimodal size-frequency histogram for both spot and croaker populations (Fig. 3.8b, c).

Per-capita predator foraging efficiency (sensu Paine 1992) was determined by quantifying the mean number of clams eaten per area ($m^2$) over the mean number of predators per area (trawl). Since crabs are the only predators able to consume whole

Fig. 3.7. (a) Mean Abundance (Number per 4-min trawl + SE) and (b) size of the common epibenthic predators blue crab, *Callinectes sapidus*, spot, *Leiostomus xanthurus*, croaker, *Micropogonias undulatus*, and hogchoker, *Trinectes maculatus*. Significant differences ($P \leq 0.05$) between samples are indicated with *. Means that are not significant are without an asterisk or indicated with ns.

## Epibenthic Predator Abundance
## York River Summer 1995




## Predator Size
## York River Summer 1995

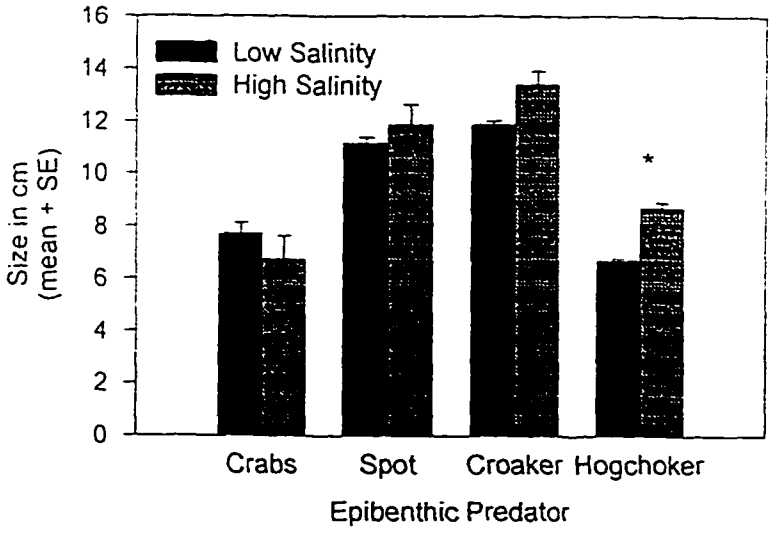


Table 3.3. Log(x+1)-transformed epibenthic predator abundance data between zones in the York River for data from four replicate 4-minute trawls in each zone (MANOVA). Multiple ANOVA models comparing predator size between zones (raw data). In parentheses is the total number of individuals collected, or the mean size in mm (SL or CL) at downriver (D) and upriver (U) zones.

| Analysis | Predator | Source of variation | SS | df | MS | F |
|---|---|---|---|---|---|---|
| MANOVA Abundance | Crabs (D: 5, U: 47) | Salinity Zone | 4.84 | 1 | 4.84 | 30.45*** |
| | | Error | 0.95 | 6 | 0.15 | |
| | Spot (D: 3, U: 20) | Salinity Zone | 3.28 | 1 | 3.28 | 30.45* |
| | | Error | 2.01 | 6 | 0.34 | |
| | Croaker (D: 2, U: 89) | Salinity Zone | 14.52 | 1 | 14.52 | 37.94*** |
| | | Error | 2.29 | 6 | 0.38 | |
| | Hogchoker (D: 18, U: 599) | Salinity Zone | 23.63 | 1 | 23.63 | 63.92**** |
| | | Error | 2.29 | 6 | 0.38 | |
| ANOVA Size | Crabs (D: 6.7, U: 7.7) | Salinity Zone | 4.41 | 1 | 4.41 | $0.58^{ns}$ |
| | | Error | 382.8 | 50 | 7.66 | |
| | Spot (D: 11.9, U: 11.6) | Salinity Zone | 1.3 | 1 | 1.3 | $1.13^{ns}$ |
| | | Error | 2.01 | 6 | 0.34 | |
| | Croaker (D: 13.4, U: 11.9) | Salinity Zone | 4.38 | 1 | 4.38 | $3.54^{ns}$ |
| | | Error | 110.2 | 89 | 1.24 | |
| | Hogchoker (D: 8.7, U: 6.7) | Salinity Zone | 69.53 | 1 | 69.53 | 26.70**** |
| | | Error | 1601 | 615 | 2.6 | |

**** $P < 0.001$; *** $P < 0.005$; * $P < 0.05$; ns $P > 0.05$.

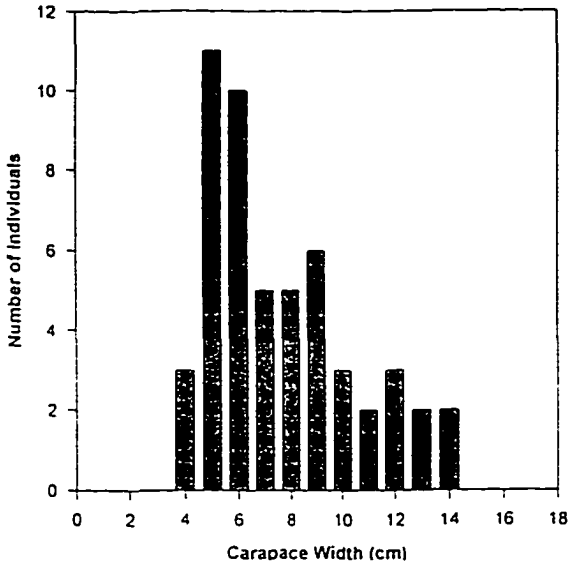
Table 3.4. Pearson correlation coefficient matrix for epibenthic predator abundance from otter trawls in the York River 1995.

| | Crabs | Spot | Croaker | Hogchoker |
|---|---|---|---|---|
| Spot | 0.81* | | | |
| Croaker | $0.36^{ns}$ | $0.63^{ns}$ | | |
| Hogchoker | $0.48^{ns}$ | $0.61^{ns}$ | 0.94**** | |
| Other | $0.24^{ns}$ | $0.48^{ns}$ | 0.97**** | 0.91*** |

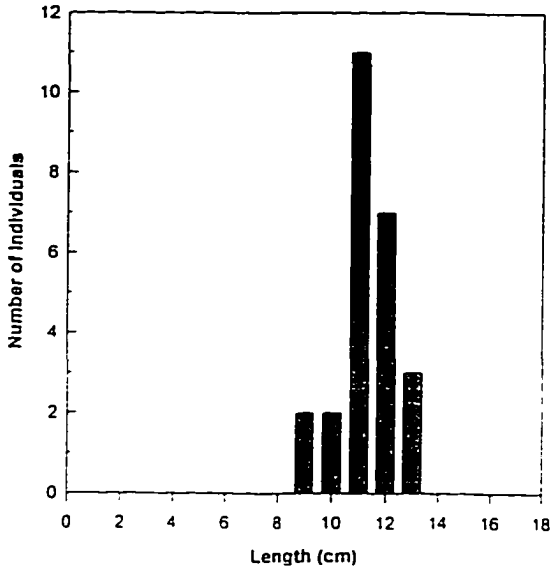
**** $P \leq 0.001$; *** $P \leq 0.005$; ns $P > 0.05$.

Fig. 3.8. Size frequency histograms of major epibenthic predators (a) blue crab, *Callinectes sapidus*, (b) spot, *Leiostomus xanthurus*, (c) croaker, *Micropogonias undulatus*, and (d) hogchoker, *Trinectes maculatus*.

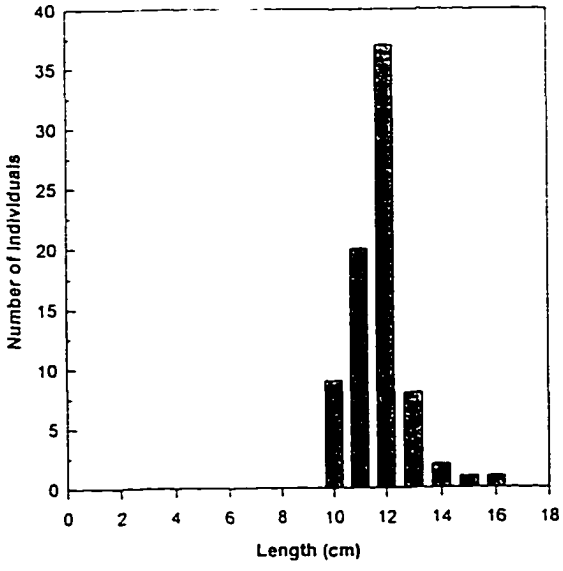
Crab



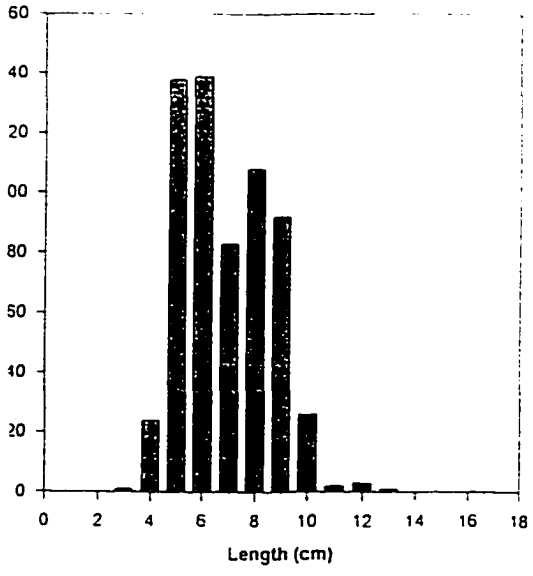

Spot




Croaker




Hogchoker



clams, per-capita foraging efficiency was calculated separately for them. For crabs upriver, the mean number of clams was 2.9, and predators was 11.75, yielding a foraging efficiency of 0.25 clams/predator. In contrast for crabs downriver, 1 clam per 1.25 predators was eaten, yielding an efficiency of 0.8 clams/predator. Although epibenthic fish do not directly consume clams, their siphon-nipping may reduce clam burying depth and indirectly cause clam mortality. If we use the total number of predators to estimate foraging efficiency, upriver there are on average 3 clams eaten per 188.8 predators, yielding an efficiency of 0.016 clams/predator. Whereas downriver, there is an average of 1 clam eaten per 7 predators, yielding an efficiency of 0.143. Though these data are limited in that estimates were made over a few months in one summer, either method used exhibits a higher per-capita foraging efficiency downriver where there are fewer predators.

## *DISCUSSION*

This study represents a field test of the effects of predation on clam survival along a salinity gradient. The results are used to infer applicability of a consumer stress model on community regulation (Menge and Sutherland 1987) in this soft-bottom ecosystem. To examine the applicability of a consumer stress model, I quantified the effect of predation upon the survival of *Macoma balthica* a key infaunal bivalve that displays contrasting distribution and abundance patterns along an estuarine gradient. I also determined the abundance of major predators in the shallow habitats of this subestuary of Chesapeake Bay.

Application of the consumer stress model in this system predicts that the importance of predation is lower in areas of higher stress (upriver, in this system) and consequently, higher abundance of *M. balthica* in upriver zones is due to lower predator-induced mortality. Although the observed patterns in diversity and environmental stress are in accord with a consumer stress model of community regulation (Table 3.5), the pattern in predator abundance and predation intensity (higher predation intensity in zones of higher environmental stress) is contrary to the model's predictions. The patterns of infaunal abundance across a broad geographic scale (~20 km) in this soft-bottom system cannot be explained by a consumer stress model. Higher stress upriver does not restrict predators from upriver areas, thus the system is probably only moderately stressed.

Table 3.5. Theoretical comparison of two benthic systems at two levels of environmental stress. Agreement between observed diversity, bivalve abundance (*Mytilus californianus* and *Macoma balthica*, for hard and soft bottoms, respectively), predator abundance, predator efficiency and prey proportional mortality. The hard bottom example comes from the rocky intertidal mid-tide exposed and protected areas which both have *Mytilus californianus* populations of varying densities. The soft bottom example comes from the York River shallow subtidal upriver and downriver zones where *Macoma balthica* is present in varying densities. Notice the discrepancies between hard and soft bottom systems for both Predator abundance and Proportional mortality of prey.

| Environmental stress | High | | Low | |
|---|---|---|---|---|
| System | Hard bottom (Exposed) | Soft bottom (Upriver) | Hard bottom (Protected) | Soft bottom (Downriver) |
| Diversity | LOW | LOW | HIGH | HIGH |
| Bivalve abundance | HIGH | HIGH | LOW | LOW |
| Predator abundance | LOW | HIGH | HIGH | LOW |
| Proportional mortality of prey | LOW | HIGH | HIGH | LOW |
| Per-capita foraging efficiency | LOW | LOW | HIGH | HIGH |

Because of this, it may be appropriate to look to other models of community regulation such as nutrient/productivity models.

The significant differences in nutrient availability point to nutrients as an important factor influencing distribution of benthos and associated predators (though this study was not designed to specifically address the effect of nutrient availability on marine benthos). Although the nutrient data presented here are limited in scope, the trend of increased carbon upriver agrees well with other, more comprehensive studies. For example, in deeper waters in the York River, percent of volatile solids increased with distance from the mouth of the York River (Dauer et al. 1989). A similar increasing trend in volatile solids was seen from downriver to upriver stations in the James River (Schaffner et al. 1987a). Thus, across the large geographic scale of this study, predators and prey may be heavily influenced by productivity. This is in accord with Menge and Olson's (1990) predictions that Nutrient/Productivity Models may govern systems on large scales, and that areas without extreme environmental stress may be governed by forces besides stress.

Predator abundance was observed to correlate with carbon productivity, thus predators may aggregate in productive areas where food is more plentiful. Predators are known to reside in habitats where food and refuge are available (Weinstein 1983). In this system, predation on infauna is important, yet predation does not drive the abundances of clams in this system. Regulation of benthos in this soft-bottom system, therefore appears to be explained by an integration of an environmental stress model (Menge and Sutherland 1987) with a productivity model (Oksanen et al. 1981, Getz 1984) resulting in a community governed through co-limitation by predators and resources (Power 1992).

A co-limitation model indicates that both top-down forces (limitation of low trophic levels by higher trophic levels) and bottom-up forces (limitation by production or resources) are responsible for community dynamics. Both nutrient enrichment and predation can be important in controlling communities as in an intertidal flat where nutrient addition increased the numbers of surface deposit feeders and predation altered the response of the benthos to enrichment (Posey et al. 1995). Plants provide the "bottom-up template", determining the number of trophic levels in a community (Hunter and Price 1992), then predation acts secondarily. Though reduced by exploitation, prey can increase with increases in their resources (Getz 1984, Arditi and Ginzburg 1989). Thus, in real food webs, a multitude of both biotic and abiotic factors regulate the relative control of communities by resource limitation versus predators (Hunter and Price 1992).

***Application of the consumer stress model to a soft-bottom system***

Natural shallow water densities of clams were higher upriver, similar to distributions documented for deep water (Boesch 1977, Holland et al. 1980, Mansour 1992) thus the first null hypothesis ($Ho_1$: There are no trends in shallow water abundances of *M. balthica*) was rejected and the alternate hypothesis retained ($Ha_1$: The natural abundance of clams in *shallow water* habitats is greater upriver, in low salinity zones). The explanation is not simply salinity preference because some downriver areas (e.g., Kings Creek), also have high and persistent clams abundances, similar to those seen upriver (R. Seitz, personal observation).

Predation (measured as number of clams killed per week) was most intense upriver, where both predators and prey abundances were highest. The mortality estimates from transplant experiments appear unbiased as they were nearly equivalent to the estimates of natural mortality (~28%/wk.). Thus, the fourth null hypothesis ($Ho_4$: There is no difference in predator-induced mortality of *M. balthica* upriver vs. downriver) was rejected and the proposed alternate also rejected ($Ha_4$: Predator-induced mortality of *M. balthica* is lower in upriver zones). Thus, a second alternate, $Ha_{4B}$: predator-induced mortality of *M. balthica* is *higher* in upriver zones, is maintained. Combining the two results, there is an inconsistency between abundance and survival of *M. balthica*; abundance is highest where survival was lowest during the study period. Furthermore, these experimental results were not consistent with the consumer stress model which predicts that predation intensity is higher in areas of decreased stress.

Based on the stress gradient, observed diversity values and predictions from the consumer stress model, the York River system lies on the high to moderate end of environmental stress (Fig. 3.1a; A = upriver, B = downriver). Downriver, diversity is greater, the effect of environmental stress is less, and that of predation should be greater than upriver (as is true for hard-bottom marine systems, Table 3.5). In contrast, predation intensity is higher upriver, refuting $Ho_4$. Thus, either my prior assumptions about a stress gradient are mistaken (as is evidence in Boesch 1977 and Dauer et al. 1993), the Menge and Sutherland model does not fit this system, or a force other than predation is most important in governing community dynamics in this system. I conclude that consumer stress is not the major factor governing community structure in this soft-bottom system.

nor is prey stress (since abundances are greatest upriver) and that other factors such as freshwater inflow (Montagna and Kalke 1992), production, or nutrient availability (Fretwell 1987, Oksanen et al. 1981, Power 1992, Menge et al. 1996) must be recognized.

Higher predation intensity upriver, in low salinities, was unexpected based on both the observed clam densities and predictions of the Menge and Sutherland Model (1987). Because previous studies have shown that in deep water habitats *M. balthica* is more abundant upriver (Boesch 1977, Holland 1985, Hines et al. 1989, Dauer et al. 1989, Mansour 1991), it is counter-intuitive that predation would also be higher there. Though this study was done in a single summer, it strongly suggests that higher abundances of clams upriver during this time period are not due to lower predation by large epibenthic crabs and fishes, so other explanations must be sought.

An attractive explanation for higher predation upriver is that the timing of this predation experiment was after a large portion of predation occurred in the downriver areas. During the winter, predators migrate out of the system or become inactive, and re-enter the rivers as temperatures increase in the spring (Lipcius and van Engel 1990). It is possible that intense predation pressure in downriver zones occurs early in the summer when the predators first move into the shallows to feed, and before my transplanting experiments began. To support this hypothesis, evidence needs to be found that predators migrate from high salinities to low, consuming and possibly depleting the supply of clams along the way.

Existing evidence for predator migration throughout the summer months, the intense predation period, do not substantiate the predator migration theory. Temporal

sampling for predators in the major tributaries of Chesapeake Bay, both deep and shallow, have not shown a slow migration upriver (Mansour 1992; Chap. 2 - this dissertation); there appears to be little seasonal effects on predator abundance from June through October (Hines et al. 1990). Predator abundance in the shallows is higher upriver as early in the summer as May (Chap. 2 - this dissertation), as predators typically enter the system quickly and move upriver immediately. Sixteen years of monitoring data in the York James and Rappahannock Rivers showed consistently higher blue crab densities upriver from May through November (Lipcius and Van Engel 1990) and many other predators follow this same pattern (VIMS trawl survey, unpublished data). Thus, differential feeding of predators early in the summer of 1995 is not probable, but is a possible explanation for the observed clam densities that remains to be tested.

Higher recruitment upriver is an additional alternative explanation of higher upriver clam abundances. Differential recruitment of invertebrate larvae can be highly dependent on currents in estuaries (Minello et al. 1989, Montagna and Kalke 1992). If upriver low salinity zones have increased larval supply, this may account for the increased observed abundances of clams there later in the summer. This hypothesis remains to be tested in the York River system. Preliminary observational sampling of juveniles within the sediment, immediately after the spring recruitment pulse in 1996 (the spring following these experiments) indicated that recruitment downriver was at least as great or greater than upriver (Seitz and Lipcius, unpublished data). If these patterns hold from year to year, recruitment does not explain the observed densities of *M. balthica*. Further examination of recruitment patterns may firmly refute a recruitment hypothesis. In addition, a complex

hydrodynamic model of the York River has been developed and may be instructive to determination of the influence of larval supply on adult abundances.

An additional explanation for higher abundances of *M. balthica* upriver is secondary dispersal or migration to higher quality habitats. Clams are able to move through the water column and redistribute from the area initially occupied by the recently metamorphosed larvae (Armonies 1992). It is postulated that active habitat selection occurs following postlarval migrations (Armonies 1994). Because upriver areas have higher detrital input and more food for deposit- or suspension-feeders (see below), these areas may be chosen preferentially as residential habitats. Under this scenario, clams settle in equal abundances upriver and downriver, but then redisperse to inhabit higher quality habitats upriver. This hypothesis could be tested by quantifying secondary dispersal or movement of juvenile clams through the water column.

An examination of the predator's per-capita foraging efficiency (number of clams killed per predator) over the limited scope of this study suggests that the consumer stress model may apply to this system. Over the weeks examined, the per-capita predator foraging rate was higher downriver with lower stress, suggesting that predators are more efficient downriver, and consistent with the idea that environmental stress can modify predation. This refutes $Ho_3$ and supports the alternate hypothesis ($Ha_3$: The efficiency of epibenthic predators in shallow water is lower in upriver zones). Increased foraging efficiency downriver suggests either that (1) consumers are more stressed upriver and thus are inefficient foragers, or that (2) mutual interference between predators reduces predation efficiency upriver (Mansour and Lipcius 1991, Mansour 1992). Thus, in accord

with the consumer stress model, consumers are potentially less efficient in higher stress, upriver zones. However, their overall impact on prey species is greater upriver, resulting in a greater importance of predation in higher stress, which conflicts with the model predictions.

The predator guild in York River shallow water was composed of mainly blue crabs, spot, croaker and hogchoker, similar to that in deeper areas (Holland et al. 1990, Mansour 1992). These dominant predators are all known to forage on clams or clam siphons, though some caught here may be too small to feed on macrofauna (Weinstein 1983). Gut content analysis of epibenthic predators from previous work shows that clams are a primary food item for crabs (Alexander 1986, Hines et al. 1990, Mansour and Lipcius 1991), and other epibenthic predators browse on clam siphons (Zwartz and Wanink 1989); thus, epibenthic predators clearly reduce abundances of clams. Abundance of these predators was higher upriver, leading to rejection of the second null hypothesis ($Ho_2$: There is no difference in the abundance of epibenthic predators upriver and downriver), and also refuting the alternative $Ha_2$. The abundance of epibenthic predators in shallow water is lower in upriver zones, because the opposite is true. *Callinectes sapidus*, *Leiostomus xanthurus* and *Micropogonias undulatus* aggregate in areas of high prey density (Hines et al. 1987, 1990), and were likely concentrating upriver in areas of increased prey abundance. The higher predation intensity upriver was therefore due to higher predator abundance upriver, rather than differences between zones in predator size composition (since this did not differ significantly between river zones).

*Models of co-limitation by predation and resources*

Predators and prey were both more abundant in upriver, low salinity, high stress areas. A probable explanation for the increase of both trophic groups in the same area may be related to productivity (Fretwell 1977, Oksanen et al. 1981, Power 1992, Menge et al. 1996). Recent data suggest that higher primary production or phytodetrital sedimentation could account for such anomalies as higher predators and prey in a certain habitat (Marsh and Tenore 1990). Menge et al. (1996) recently showed a similar pattern in some rocky intertidal communities. At one experimental site, there was higher productivity, wave stress, and abundances of both predatory starfish and their major prey, mussels, as compared to another experimental site with lower stress. Data were consistent with the notion that differences in phytoplankton productivity generated between-site differences, suggesting that bottom-up factors (prey recruitment, growth , and abundance) determined variation in the strength of a top-down factor (predation).

Nutrient loading and transformation into food for marine benthos can lead to increases in abundance and biomass of infauna (Montagna and Yoon 1991). Freshwater inflow may have negative effects such as sedimentation, resuspension and advection, and losses due to low-salinity tolerances of organisms, or positive effects such as enhanced productivity, and recruitment gains (Montagna and Kalke 1992). When two Gulf coast estuaries were compared, macrofauna densities increased with increasing freshwater inflow (Montagna and Kalke 1992). Thus, freshwater inflow is important to those species that can survive in low salinity. The few species that can tolerate low salinity take advantage of high inflow for increased productivity

Nutrient and Productivity models have been developed for various systems (Fretwell 1977, Oksanen et al. 1981, Power 1992). In these models, plants in relatively unproductive systems do not produce enough energy to support the herbivores in the community, and the community is thereby controlled by interspecific competition. In productive systems, energy is sufficient to support both herbivores and carnivores, consequently increasing the importance of predation in community regulation. In this case, nutrient or productivity levels determine trophic complexity rather than environmental stress (Menge and Olson 1990). The prediction is that increased productivity will increase the importance of predation in herbivore regulation (Oksanen et al. 1981).

In the York River, upriver habitats may offer more food and therefore may be higher quality habitats. Sedimentary carbon is significantly higher upriver (Chap. 2 - this dissertation) and standing stock phytoplankton, chlorophyll *a* is higher upriver (Rennie and Nielson 1991), suggesting that these areas may provide abundant food. Although chl *a* and production are not the same, higher chl *a* in the water column typically means more production reaching the benthos (Valiela 1984). High predator density occurred where prey abundances were greater. Perhaps a difference in primary productivity, or a "bottom-up" factor (Menge 1992, Power 1992), associated with riverine inflow can account for the higher abundance of both predators and prey upriver in the York River system. These potentially interesting effects of primary production on predator and prey abundance provide the cornerstone for future studies on predator-prey interactions in the York River looking at the influence of both top-down and bottom-up forces on population dynamics.

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## DISSERTATION SUMMARY

In summary, this investigation compiled existing theoretical models of community regulation, experiments on species diversity and changes due to predator exclusion, as well as experiments on survival of the clam *Macoma balthica* along an estuarine salinity gradient. The investigations herein resulted in a modification of the MS model, to incorporate soft-bottom systems, an understanding that the effects of predation on benthic diversity are stronger upriver than downriver in the York, and, consistent with results for community diversity, the effects of predation on transplanted *M. balthica* were greater upriver than downriver.

Experiments on controlling forces in soft-bottom systems have advanced our knowledge substantially but still haven't resulted in a unifying model of community regulation that can be applied to all benthic systems -- hard substrates and soft substrates alike. The Menge and Sutherland (1987) model can be modified to incorporate all systems if we include the notion that all habitats do not have equivalent resource availability, thus the effect of recruitment will be different depending on whether or not there is competition for a limiting resource. This concept can be incorporated into the MS model by changing the recruitment axis to a recruitment to resource ratio. In soft bottoms, where the space resource is plentiful, the recruitment to resource ratio will typically be low, and competition of little importance. In contrast, in hard-bottom

habitats, where space is limited, when recruitment is high, the recruitment to resource ratio is also high, leading to competition. The different recruitment to resource ratios lead to different predictions for the importance of structuring forces.

Though baseline benthic diversity was driven by salinity (with higher diversity downriver, closer to oceanic influence), higher stress upriver did not effect the ability of consumers to feed, as the effects of predation on benthic diversity were greater upriver where predator abundance was also greater. Sedimentary carbon and nutrients were also greater upriver, leading to greater benthic production that could be transferred through higher trophic levels. The stress imposed by a salinity gradient is not great enough to adversely effect predators, but instead, the effect of a production gradient overrides the physical stress. The system appears to be driven by 'bottom up' forces that allow higher abundances of both prey and predators in areas of higher productivity (e.g., upriver).

At the population level, the effect of predation was greater upriver, similar to that seen for diversity. Elevated predation upriver was due to higher quality food availability upriver (e.g., abundant clams). The distribution of the dominant clam, *M. balthica*, was driven by the availability of its food, subsequently increasing benthic production and biomass available to consumers. The predators appear to follow the prey, thus the system is driven by primary production, not physical stress. Therefore, when physical stress is low to moderate, it does not control community structure, but instead, the system is driven by food availability which increases the interactions in the food chain at higher productivity. As productivity increases, the complexity of the food chain increases, heightening the importance of predation. Mutual interference of predators allows

inefficient predation upriver, allowing some prey to survive, hence, the system is driven by a combination of top-down and bottom-up forces.

# VITA

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Rochelle D. Seitz was born in Chicago, Illinois, 21 November 1964, and graduated from Evanston Township High School in 1982. She earned a Bachelor of Arts in Biology from Colgate University in Hamilton, New York, in 1986. She received her Master of Arts in Marine Science at the School of Marine Science, The College of William and Mary in 1991, and entered the doctoral program at the School of Marine Science, The College of William and Mary in 1991.